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THE ECOLOGICAL DISTRIBUTION OF SPIDERS IN NON-FOREST MARITIME COMMUNITIES AT BEAUFORT, NORTH CAROLINA

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INTRODUCTION

Spiders as a group constitute one of the best indexes for the investigation of community structure, stratification and succession of animals. The great degree of adaptive radiation which the order has undergone has resulted in their filling almost every ecological niche. The abundance of spiders makes quantitative sampling relatively simple and the resulting statistics are of a workable numerical order; yet at the same time the group is not so large that a working taxonomy is beyond the capabilities of a single investigator. Despite these facts, there have been very few ecological studies made of spiders, particularly in the field of synecology.

Elliot (1930) studied the ecology of the spiders of a beech-maple forest in southern Indiana. The 99 species he reported were stratified within the community, this stratification being correlated with environmental conditions within the vegetation. He also reported a seasonal succession of species with population peaks occurring in late spring and early fall. Jones (1946), who was primarily concerned with the inter-stratal migrations of various seasons, found a similar stratification of the spider population in her study of the invertebrates of an Illinois woodland.

Truman (1942) investigated the ecology of the spider fauna of Presque Island in Lake Erie. He concluded from his study of this small island that "most of the spider species present are rather definitely associated with one or another of the plant associations and their ranges may be expected to change as the plant associations progress".

Perhaps the greatest contribution to the synecology of spiders, particularly from the quantitative aspect, has been made by Lowrie (1942 and 1948) through his studies of the xeric dunelands on the southern shore of Lake Michigan. The earlier paper was a general study of the distribution of the species present in the area and the probable limiting environmental factors. Concerning the latter he concluded that low moisture content, high temperature, and wind velocities were most important in restricting the distribution of spiders in that area.

In his later paper Lowrie approached the ecology of the spiders of the region from the standpoint of the zonation and succesion of the plant communities extending back from the Lake shore. He found a distinct increase in numbers and densities of species with proximity to the beech-maple climax. He correlated this zonation of the spider population with decrease in evaporation and temperature and increase in stratification as the communities became more mesophytic with proximity to the climax forest.

The most recent ecological study of spiders has been that of Muma & Muma (1949) who investigated the mixed prairie communities in Nebraska by means of quantitative pitfall and litter sampling. They found that the prairie spider populations exhibited not only seasonal but also daily vertical migratory movements.

As far as can be determined, however, no ecological

study has ever been made of the spiders of the maritime provinces. For this reason the present investigation was undertaken on the coast of North Carolina during 1951 and 1952, the purpose being to determine the population structure of the spiders living in the major maritime communities and their relationship to the ecological succession of the coastal vegetation. The numerous bays, sounds and estuaries of this region have produced varied and broad expanses of maritime vegetation which provided an excellent location for such a study.

The author wishes to thank Dr. I. E. Gray of the Duke University Zoology Department for his guidance, suggestions and criticism throughout all phases of this study. To Dr. W. J. Gertsch of the American Museum of Natural History for his aid with various taxonomic problems and to the Duke University Marine Laboratory for the many facilities extended during the course of this investigation the author is also very grateful.

REGION AND CLIMATE

The area in which this study was undertaken is located on the coast of North Carolina in the Beaufort-Morehead region of Carteret County, seventy miles southwest of Cape Hatteras.

Geologically, the sands of the North Carolina coast represent the last and the youngest of the six coastal plain terraces laid down during the period from the Pliocene to the Pleistocene and much of the present topography has been formed in recent times.

This topography is characterized by many sounds, bays, and estuaries produced by a series of protecting sand bars, the outer banks, which extend in a chain down the coast. In the Beaufort region, these outer banks run in an east-west direction. Shackleford Banks, which is the shortest member of the chain, extends toward Core Banks on the east and Bogue Banks on the west, the latter being separated from Shackleford by the Beaufort Inlet (Fig. 1).

Behind these banks lie three narrow sounds, Core, Back, and Bogue. By their many extensions into the mainland these sounds have created innumerable bays, estuaries and acres of marshes. Beaufort lies between the two largest estuaries, Newport and North Rivers.

In general the climate of Beaufort is intermediate between that of southern and northern coastal areas such as Nantucket, Mass. and Jacksonville, Fla. During the year 1951 Nantucket had eighty days in which the temperature was 32°F. or below; Beaufort had twenty-one and Jacksonville nine. There is no distinct precipitation pattern for the area.

THE MARITIME PLANT COMMUNITIES

The maritime communities with which this study is concerned are those plant communities in which the presence of the species is directly or indirectly determined by salt water. In the Beaufort region there are nine principal major maritime communities in addition to a number of lesser ones. Of these nine, three are intertidal: *Spartina alterniflora*, Spartina-Distichlis-Salicornia, and *Juncus roemerianus*. The remaining six are above the high tide mark. Two are grass communities, *Spartina patens* and *Uniola paniculata;* one, a mixed herbaceous community; two

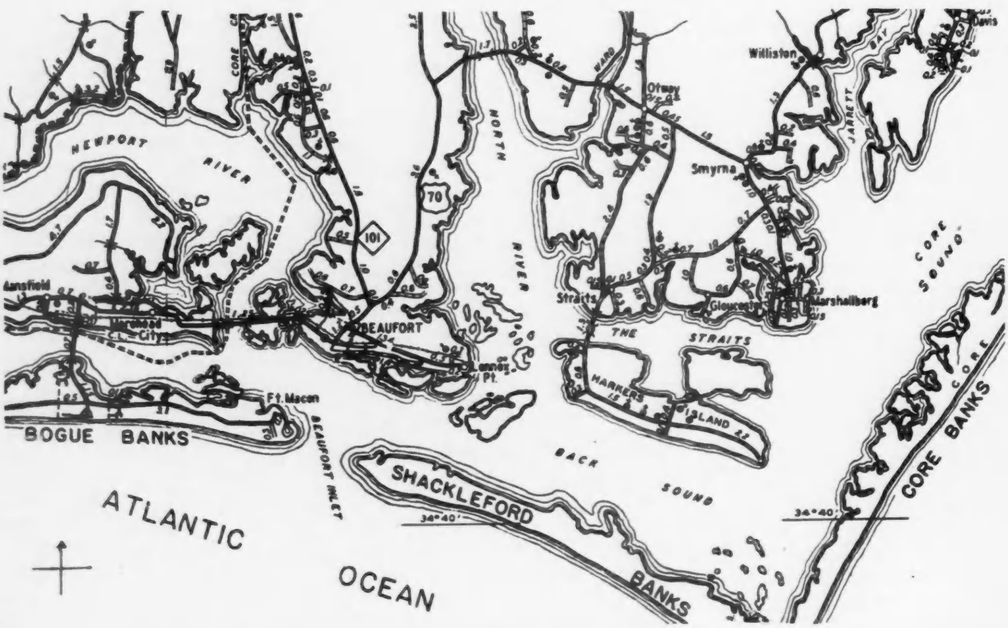

FIG. 1. Map of the south middle portion of Carteret Co., N. C.

shrub communities, Myrica-Ilex-Quercus and Persea-Ilex-Quercus; and the maritime forest. All except the last are included in this study.

It should be pointed out that while these communities are typically maritime, they are not, except for Uniola, characteristic of the ocean front which is subjected to heavy salt spray, but rather are found on the lee side of the fore dunes and particularly along the more protected sounds.

The primary factor influencing the occurrence and distribution of maritime communities is the amount of sea water with which the plant is in contact. This factor has been called "hydroperiod" by Wells (1928), who made one of the first ecological studies of North Carolina coastal vegetation. The degree of hydroperiod, therefore, determines the presence or absence of the maritime communities. At one extreme the hydroperiod may be very long, continually flooding the community with sea water. Intertidal communities such as *Spartina alterniflora* are subjected to such continual and long hydroperiods. At the opposite extreme is the sand dune community of Uniola, sea oats, which is so high above the tidal fluctuating water table that a saline hydroperiod is actually nonexistent.

Not only the length of the hydroperiod but also the degree of salinity is an important factor influencing the plant communities. *Spartina alterniflora* is little affected by low salinities, being quite prevalent even in brackish water. On the other hand, the large tracts of *Juncus roemerianus* are most frequently found in the upper tidal limits of more brackish areas where salinities are low and flooding is much less rhythmic.

With the factor of hydroperiod in mind it will immediately be seen that as the distance back from the high tide mark increases there is a steady decrease in the saline hydroperiod. Thus, if the presence or absence of plant species is determined by the degree of hydroperiod, there will also be a marked change in the vegetation with increasing distance above the high tide mark. This results in a zonation of vegetation which is characteristic throughout coastal areas.

Taking as an example a hypothetical area, the intertidal zone with a long hydroperiod is characterized by the grass, *Spartina alterniflora*. At the high tide mark the *Spartina alterniflora* zone abruptly ends and a belt of *Spartina patens* begins. In the latter zone there is a much shorter hydroperiod for although the tidal water table is only a short distance below the surface, flooding occurs only rarely during the very high spring tides. A drift line is usually found between these two zones of Spartina.

As the zone of *Spartina patens* extends back from the high tide mark there is a continual decrease in the saline hydroperiod. This decrease is due to the increasing depth of the tidal water table as the ground surface becomes higher which allows the appearance of numerous other plant species resulting in a third zone of a mixed herbaceous nature. This community is characterized by a number of species with the grasses, *Spartina patens*, *Andropogon littoralis* and *A. glomeratus* and Panicum still dominant; in addition the composites Solidago, Aster and Eupatorium are also typical.

Following the mixed herbaceous zone there is a shrub zone dominated by the wax myrtle, *Myrica cerifera*, but always accompanied in greater or lesser abundance by the holly, *Ilex vomitoria*, and live oak, *Quercus virginiana*.

With further decrease in the hydroperiod the shrub zone undergoes marked changes. In contrast to the preceding community this shrub complex is very compact creating a canopy of vegetation which so sharply reduces the penetration of light that there is almost no undergrowth and the leafy branches of the shrubs are restricted to the top. In addition there is a much heavier deposition of litter. Oak and holly are more abundant here and Myrica, except in low spots, is more or less replaced by the bay, Persea.

The zonation ends with the maritime forest, where large live oak trees are dominant.

Such a well developed and complete series of all zones never exists in any one place and sharp distinctions between zones are found only in those communities near the water. Nevertheless, the fundamental ecology of maritime vegetation is one of zonation.

The above description of maritime zonation would apply to coastal vegetation at any given moment in time. The hydroperiod of any particular area, however, will change over a long period of time, and in situations with long hydroperiods there will ordinarily be a tendency for decrease in length. It should be pointed out, however, that the degree and direction in time of the hydroperiod change depend entirely on physiographic conditions.

If, for example, water currents, prevailing winds and other physiographic factors favor a deposition of mud and sand onto an intertidal zone, the hydroperiod will decrease and over a long period of time the upper limits of the *Spartina alterniflora* will shift to a *Spartina patens* community. However, depending on physiographic conditions it is entirely possible for the reverse to occur.

Thus, it would be quite accurate to say that what is zonational in maritime communities at any given moment in time, can actually be successional over a period of time. It is important to remember that the term succession can be used only in a physiographic sense, for here the causal factor is the change in hydroperiod rather than one stage in itself creating the biological conditions necessary for the initiation of the next. Figure 2 illustrates both maritime zonation and succession in this coastal area.

The relationship of three communities, *Uniola paniculata*, Spartina-Distichlis-Salicornia and *Juncus roemerianus*, included in this paper, is not very well understood and they do not fit clearly into the successional picture described above.

Sea oats, *Uniola paniculata*, is very abundant in the Beaufort region particularly along the ocean front foredunes and on sand dunes along the sound. This grass is the initial plant on bare dry sand and

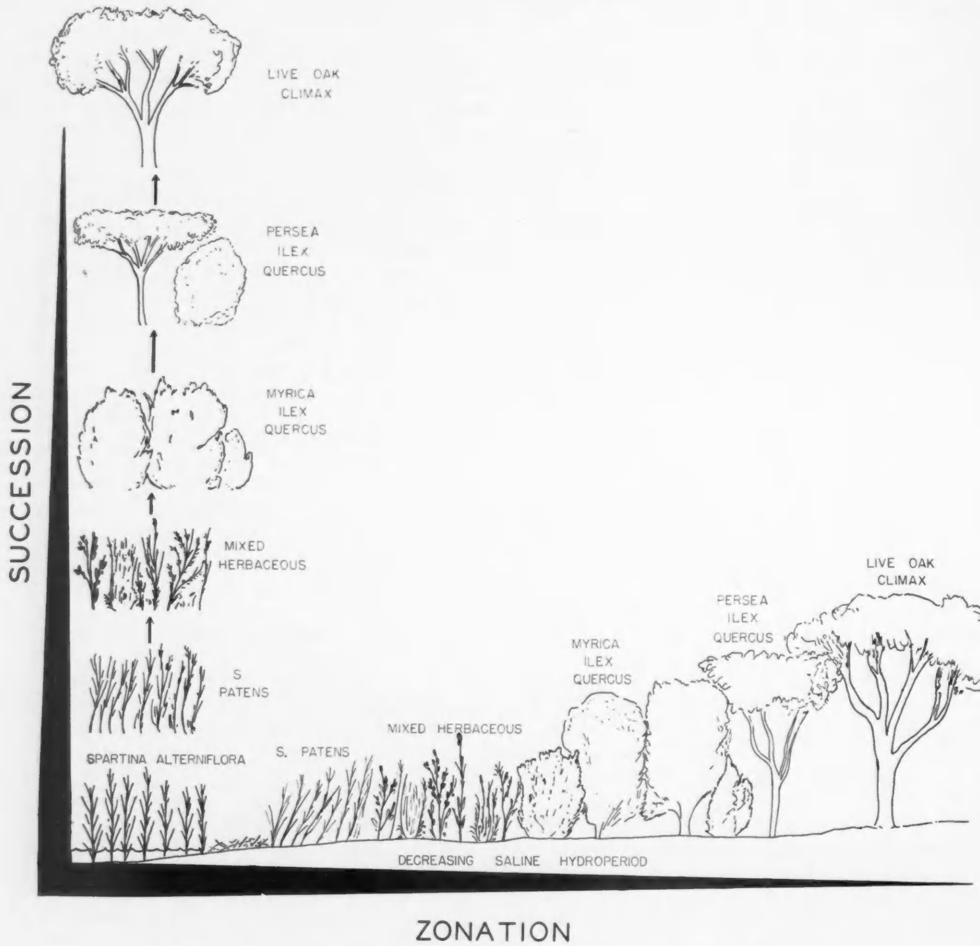

FIG. 2. Diagram of the zonation and succession of maritime vegetation.

is important as a stabilizer of shifting dunes but the subsequent succession is not clear. Many older stands contain a large amount of Andropogon and it is quite possible that an area well stabilized with Uniola and sufficiently far back from the ocean front may shift to a mixed herbaceous community and then to the maritime shrubs.

Spartina-Distichlis-Salicornia and *Juncus roemerianus* are both intertidal communities forming distinct zones back from the water beginning with pure Spartina. Although they must be considered maritime communities, they are strictly estuarian in their greatest development and usually occur in only very small isolated stands along the sounds. The supratidal succession along estuaries does not follow the series of communities already described but rather tends to move in the direction of the bordering pine savannas.

In choosing examples of maritime communities for study every attempt was made to select stands of each type which were as large and as pure as possible. The stands selected were located at the following stations:

Station 1 contained two communities, *Spartina alterniflora* and *Spartina patens*, located on the last

FIG. 3. Point of transition between *Spartina alterniflora* (left) and *Spartina patens* (right).

FIG. 4. The sand-binding dune grass, *Uniola paniculata* (sea oats), on Piver's Island.

of a series of marsh islands extending north of Highway U. S. 70 between the Beaufort and Morehead bridges in the Newport estuary (Fig. 3).

Station 2 was a sea oats community, *Uniola paniculata,* located on a series of small sand dunes along the southeast margin of Piver's Island between Beaufort and Morehead City (Fig. 4).

Station 3 was located at the North River Experimental Oyster Farm on the North River estuary off U. S. 70, six and one half miles north of Beaufort. This area consisted of large expanses of salt marsh made up of three zones beginning at the river margin, *Spartina alterniflora,* Spartina-Distichlis-Salicornia, and *Juncus roemerianus* (Fig. 5). All of these communities lie in the intertidal zone but flooding here is much less rhythmic and the salinity is variable. Both the degree of flooding and salinity is more-or-less dependent on rainfall which will raise and lower the level of the North River estuary.

FIG. 5. *Juncus roemerianus* zone at North River estuary.

Station 4, located on the southwest corner of Carrot Island between Horse Island and Taylor's Creek channel one mile south of Beaufort, contained two communities: a Myrica-Ilex-Quercus shrub community surrounding two large stands of a mixed herbaceous nature (Figure 6).

Station 5, containing a Persea-Ilex-Quercus shrub community, was located on the lee side of the foredunes 1.6 miles west of Atlantic Beach on Bogue Banks.

In addition to the stands of *Spartina alterniflora* described above where the majority of the work was carried out, samples from this community were also taken in the following localities in Carteret County:

FIG. 6. Mixed herbaceous (foreground) and Myrica-Ilex-Quercus shrub communities (background) on Carrot Island.

marsh islands in Back Sound; Town Marsh, Beaufort; east side of North River off U. S. 70; east side of Lennox Point three miles south of Beaufort; northwest and north middle side of Harker's Island; by clam factory at Williston.

MATERIALS AND METHODS

In studying the spiders of maritime communities emphasis was placed on quantitative methods of sampling as far as possible. These consisted of sweeping, pitfall traps and hand sampling.

Sweeping was used to sample the population living in the upper parts of vegetation. For this purpose a sweep net was employed with a net diameter of sixteen inches and a three foot handle. Each stroke covered a three foot arc through the vegetation and the return stroke was always swept over the same area as the first. A single step forward was then taken and two more strokes were made in the same manner. A single sweeping unit was established at two hundred strokes and the second hundred strokes were carried out over the same area as the first. This resulted in each portion of the vegetation covered being swept four times: Thus the more tenacious species were less likely to be missed.

In sweeping shrubs this method had to be slightly modified. Owing to the rigidity of shrub growth it was almost impossible to pass the net through the vegetation. The net was, therefore, held stationary and a mass of leaves and branches were twice beaten very hard into the net. The second hundred strokes were again carried out over the same shrubs as the first. This modification probably introduced some error in comparing shrub and herbaceous communities, but certainly far less than if the usual sweeping method had been employed.

Following each sweeping unit the sample collected with the accompanying vegetation debris was placed in a large plastic bag. This was returned to the laboratory and the contents sorted over a large piece of cloth.

The ground cursorial forms were collected by means of pitfall traps. These traps consisted of small wide mouth jars with a lip diameter of $2\frac{1}{8}$ inches. The jar was filled one-third full of 50 per cent alcohol and buried so that the lip was flush with the ground level. The traps were then left in place for forty-

eight hours before being removed. A sample unit was established as the combined contents of four jars and total sampling was limited to ten units. Since twenty traps were always buried in a community in one day, and twenty on the next day, the four jar sample unit consisted of combining the contents of the first two jars of one day with the first two of the next in order to negate any error brought on by environmental factors.

The secretive species of spiders were collected by two methods. Those living in leaf mold were sifted out by means of a Berlese funnel. A sample unit consisted of one square foot of litter and humus marked out with a metal frame.

Many secretive forms live around roots and within the bases of plants. These were collected by digging up a clump of plants and shaking the roots and bases over a white sheet. A sampling unit in this case was established as fifteen minutes of collecting time.

The quantitative sampling described above was carried out in such a manner that the results could be expressed in terms of frequency and density, these two expressions allowing the best comparison of the population of different communities.

Frequency, as used in this study, is a statistical expression of the number of times a particular species occurs in a given number of samples, all of which have been taken in the same concrete community. Density, on the other hand is the average number of individuals of a species per sample. As an example, if ten samples were taken in a particular habitat and twenty individuals of a species A were collected in the first sample and none in the remaining nine, this species would have a frequency of ten percent and a density of two, i.e., an average of two per sample. It is the belief of this author that this use of the term "density" results in a more accurate expression of the spider population than its frequent use as the percentage of the total number of that species relative to the total number of spiders collected in all ten samples. This is particularly true in population of very low density.

The term "constancy" was used in studying the abstract *Spartina alterniflora* community. The abstract community represents the sum total of all the stands of a certain type of community without considering any one stand in particular. Thus one can think of a particular stand of pine subclimax in a certain location or one can think of the pine subclimax in general. The former would be a concrete pine community while the latter would represent the abstract pine community.

Constancy, like frequency, refers to the number of times a certain species occurs in a given number of samples. It differs from frequency, however, in that each sample is taken from a *different* stand of the abstract community while frequency refers to samples, all of which have been taken in the *same* stand. Thus constancy bears the same relation to the abstract community as does frequency to the concrete community.

Within a community the spider population falls into a number of diverse ecological groups: web-builders and hunters in the upper stratum of the vegetation, cursorial species at the ground level and secretive forms in the leaf mold. This then necessitates different sampling methods for each ecological group. Since the frequency and density of two populations are not comparable unless sampling methods are identical, comparisons only of the same ecological group in different communities can be made. This means that while the ground fauna of two different communities are comparable quantitatively, the same is not true of the litter population and the ground population of the same community.

The size of the sample for any method was always established by means of the species-area curve and was always established in that community with greatest density. This size was then taken as the standard sample unit and used for comparison in all other communities of lesser density.

Ideally, from the standpoint of comparison, samples from each community should be taken on the same day. This, however, was found to be impossible. The two stations that could be reached by car were twenty miles apart and two other stations could be reached only by boat. Thus, in order to take only one sweeping sample from each community a full day would be required. This would not include the equal amount of time involved in sorting the material which must be done immediately or shortly after it is collected.

In addition to the quantitative methods some non-quantitative sampling was also carried out. Some shrub species were collected by spreading a sheet on the ground and beating the branches above with a stick. The spiders that had fallen onto the sheet were then collected. Also, two large pitfall traps, as described and designed by Ficter (1941), were employed during the summer of 1951.

The cursorial wolf spiders which are largely nocturnal were also collected by means of a headlight. The eyes of this family reflect light and even small individuals can be located at a distance of fifty feet.

In all cases the contents of each sample both qualitative and quantitative were identified, recorded separately and the total numbers of males, females and immatures of each species listed. Representative specimens of all species collected have been deposited in the collections of the American Museum of Natural History.

Although the most intense collecting was carried out during the summers of 1951 and 1952, samples were taken once in each habitat during each month of the fall, winter and spring of 1951 and 1952 with the exception of December and February.

RESULTS

A total of 139 species of spiders belonging to 24 families were collected in non-forest maritime communities at Beaufort, N. C. These species, listed by family, appear in Table 1.

TABLE 1. List of the spiders collected in non-forest maritime communities at Beaufort, N. C.

Atypidae
Atypus bicolor Lucas
Ctenizidae
Pachylomerides audounini (Lucas)
Segestriidae
Ariadna bicolor (Hentz)
Pholcidae
Psilochorus pullulus (Hentz)
Spermophora meridionalis Hentz
Theridiidae
Allotheridion australe (Banks)
Allotheridion chinda (Chamberlin and Ivie)
Allotheridion dividuum (Gertsch and Archer)
Allotheridion lyricum (Walckenaer)
Allotheridion murarium (Emerton)
Ancylorrhanis hirsutum (Emerton)
Anelosimus textrix (Walckenaer)
(=*A. studiosus* (Hentz))
Coleosoma normale Bryant
Conopistha nephilae (Taczanowski)
Conopistha partita (Walckenaer)
(=*C. cancellata* (Hentz))
Euryopis limbata (Walckenaer)
Latrodectus mactans (Fabricius)
Paidisca marxi (Crosby)
Rhomphaea lacerta (Walckenaer)
(=*R. fictilium* (Hentz))
Theridula sphaerula (Hentz)
Tholocco pallida (Emerton)
Nesticidae
Nesticus pallidus Emerton
Linyphiidae
Frontinella pyramitela (Walckenaer)
(=*F. communis* (Hentz))
Meioneta beaufortensis Barnes
Meioneta grayi Barnes
Tapinopa bilineata Banks
Tennesseellum formicum (Emerton)
Micryphantidae
Ceraticelus anomalus Gertsch
Ceraticelus laetabilis (O. P. Cambridge)
Ceraticelus paschalis Crosby and Bishop
Ceratinopsis nigriceps Emerton
Ceratinopsis swanea Chamberlin and Ivie
Eperigone albula Zorsch and Crosby
Eperigone banksi Ivie and Barrows
Eperigone maculata (Banks)
Erigone autumnalis Emerton
Grammonota gallinoides Barnes
Grammonota maculata Banks
Grammonota sclerata Ivie and Barrows
Grammonota trivittata Banks
Scylaceus pallidus (Emerton)
Epeiridae
Acacesia foliata (Hentz)
Acanthepeira stellata (Walckenaer)
Allepeira lemniscata (Walckenaer)
Argiope aurantia Lucas
Argiope trifasciata (Forskal)
Conepeira bivittata (Walckenaer)
Conepeira dawsoni Archer
Epeira pegnia Walckenaer
Eustala anastera (Walckenaer)
Gasteracantha elipsoides (Walckenaer)
(=*G. cancriformis* (Linneus))
Larinia directa (Hentz)
Mangora floridana Archer
Micrathena gracilis (Walckenaer)
Neoscona minima F. Cambridge
Singa keyserlingi McCook
Singa rubens (Hentz)
Tetragnathidae
Leucauge venusta (Walckenaer)
Tetragnatha caudata Emerton
Tetragnatha pallescens F. O. P. Cambridge
Mimetidae
Mimetus puritanus Chamberlin
Agelenidae
Agelenopsis emertoni Chamberlin and Ivie
Agelenopsis naevia (Walckenaer)
Hahniidae
Hahnia cinerea Emerton
Pisauridae
Dolomedes albineus Hentz
Pelopatis undulata (Keyserling)
Pisaurina mira (Walckenaer)
Thanatidius tenuis (Hentz)
Lycosidae
Arctosa funeva Gertsch
Arctosa funerea (Hentz)
Arctosa littoralis (Hentz)
Geolycosa pikei (Marx)
Lycosa annexa Chamberlin and Ivie
Lycosa carrana Bryant
Lycosa lenta Hentz
Lycosa modesta (Keyserling)
Lycosa rabida Walckenaer
Pardosa floridana Banks
Pirata apalacheus Gertsch
Pirata suwaneus Gertsch
Schizocosa crassipes (Walckenaer)
Schizocosa episma (Chamberlin)
Schizocosa salsa Barnes
Trochosa abaita (Gertsch)
Trochosa shenandoa Chamberlin and Ivie
Oxyopidae
Oxyopes salticus Hentz
Peucetia abboti (Walckenaer)
Gnaphosidae
Cesonia bilineata (Hentz)
Drassyllus adocetus Chamberlin
Drassyllus aprilinus (Banks)
Drassyllus creolus Chamberlin and Gertsch
Drassyllus ostegae Chamberlin
Gnaphosa sericata (L. Koch)
Poecilochroa capulata (Walckenaer)
Poecilochroa famula (Chamberlin)
Poecilochroa unimaculata (Emerton)
Zelotes hentzi Barrows
Clubionidae
Agroeca pratensis Emerton
Castianeira amoena (C. Koch)
Castianeira trilineata (Hentz)
Castianeira vulnerea Gertsch
Chiracanthium inclusum (Hentz)
Clubiona littoralis Banks
Clubiona pallens Hentz
Clubiona plumbi Gertsch
Meriola decepta Banks
Micaria browni Barnes
Phrurotimpus alarius (Hentz)
Phrurotimpus illudens Gertsch
Scotinella pintura (Ivie and Barrows)
Anyphaenidae
Aysha gracilis (Hentz)
Oxysoma cubana Banks
Teudia fragilis (Banks)
Thomisidae
Misumenops delphinus (Walckenaer)
(=*M. celer* (Hentz))
Philodromus undarum Barnes
Tibellus duttoni (Hentz)
Tmarus rubromaculatus Keyserling
Xysticus fraternus Banks
Salticidae
Agassa cerulea (Walckenaer)
Gertschia noxiosa (Hentz)
Habrocestum pulex (Hentz)
Habronattus agilia (Banks)
Hentzia ambigua (Walckenaer)
(=*H. palmarum* (Hentz))
Hyctia bina (Hentz)
Hyctia pikei Peckham

Neonella vinnula Gertsch
Onondaga lineata (C. L. Koch)
Paraphidippus marginatus (Walckenaer)
Phidippus fraudulentus (Walckenaer)
Phidippus rimator (Walckenaer)
Phidippus whitmanii Peckham
Thiodina iniquies (Walckenaer)
(= *T. sylvana* (Hentz))
Zygoballus bettini Peckham
Lyssomanidae
Lyssomanes viridis (Walckenaer)
Dictynidae
Dictyna gloria Chamberlin and Ivie
Dictyna savanna Chamberlin and Ivie
Lathys albida Gertsch
Lathys maculina Gertsch
Uloboridae
Uloborus glomosus (Walckenaer)
(= *U. americana* (Walckenaer))

Spartina alterniflora

The spider population of the intertidal grass, *Spartina alterniflora*, is confined to the upper part of the stems and leaves. The first sampling in this community was carried out at Station 1 from May through September 1951. The results from ten sweeping units showed a total of fourteen species of spiders living in this intertidal grass (Fig. 7). Three of these species had densities that were far greater than the total of all the remaining members of the population. *Grammonota trivittata* was most abundant with a frequency of 100% and a density of five individuals per unit sample. *Dictyna savanna* and *Eustala anastera* followed in somewhat lower numbers. *Singa keyserlingi* was fourth in order of population size but could not approach the magnitude of any of the first three species.

With the exception of five species all spiders taken in this series of samples were web-builders, including the three major species.

A second series of ten sweeping units was taken in the same stand from May through June 1952. The same essential structure of the population was found to be present as during the preceding year but with a sharp reduction in density (Fig. 8). *Grammonota trivittata* underwent the greatest drop while *Eustala anastera* fell slightly behind *Singa keyserlingi.* It should be noted, however, that despite the reduction and reorientation in density magnitudes the same three species made up the major part of the community. Of the hunting spiders only three species were present with *Hyctia bina* somewhat replacing *Poecilochroa unimaculata* in density. The latter did not appear at all in this series of samples.

Monthly sweeping samples were taken in this stand of *Spartina alterniflora* during the winter of 1951-52. Of the four major members of the community *Gram-*

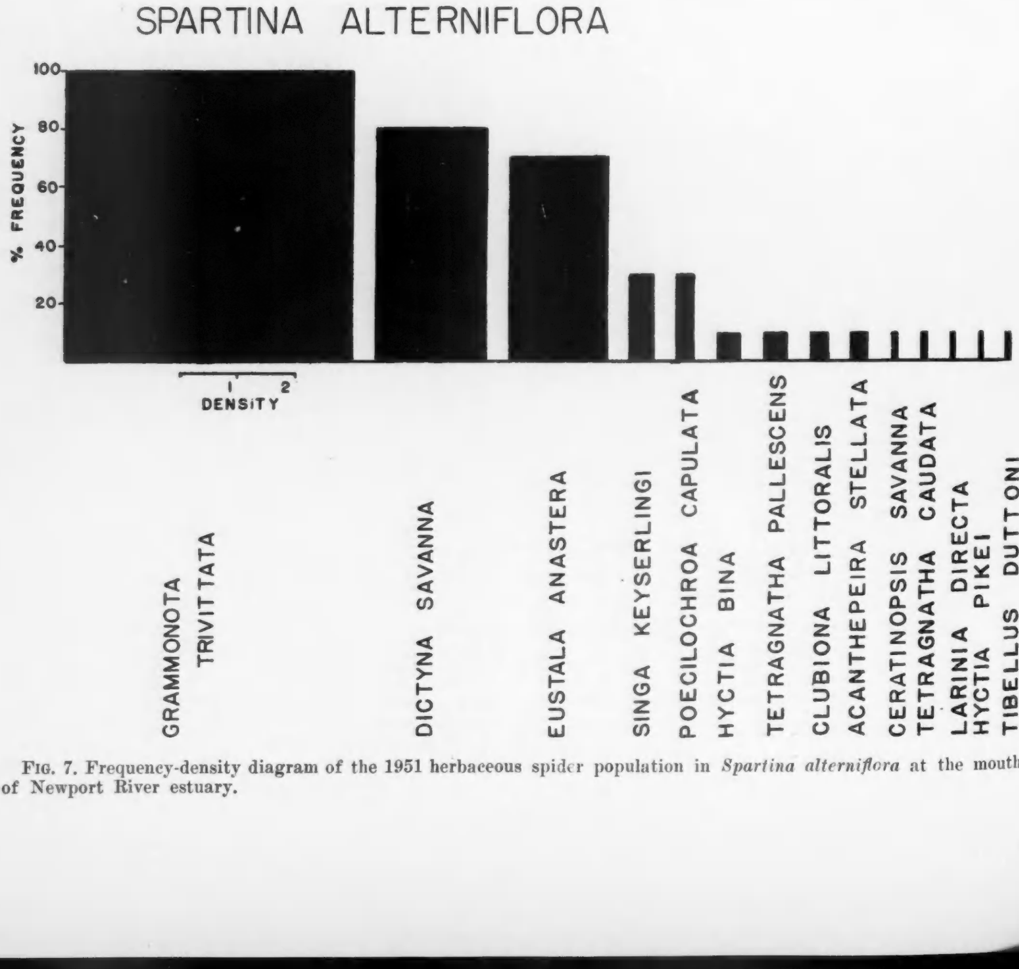

FIG. 7. Frequency-density diagram of the 1951 herbaceous spider population in *Spartina alterniflora* at the mouth of Newport River estuary.

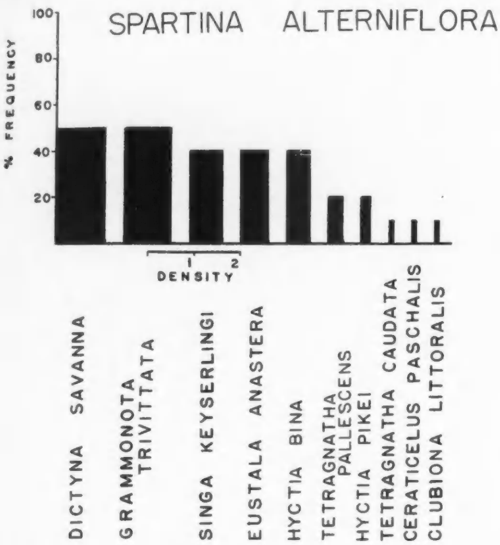

FIG. 8. Frequency-density diagram of the 1952 herbaceous spider population of *Spartina alterniflora* at the mouth of Newport River estuary.

monota trivittata was the only species which did not undergo a sharp drop in density during the colder months. *Dictyna savanna* and *Singa keyserlingi* disappeared entirely, while *Eustala anastera* reached a very low density. In March Dictyna and Singa began to reappear and the whole population rapidly reassumed its normal summer structure.

In May and June 1952 ten sweeping units were taken in a stand of *Spartina alterniflora* at North River (Station 3). It should be reiterated that the environmental conditions here are somewhat different from those at Station 1. The Spartina at North River is more protected, the salinity is more variable and the grass is subjected to much less tidal flooding.

The results of sampling in this stand showed an extremely marked abundance of the orb-weaver, *Eustala anastera* (Fig. 9). The density of 9.4 was far greater than that ever found in the preceding stand. *Grammonota trivittata* and *Dictyna savanna* again made up an important part of the total population but were far overshadowed by the abundance of Eustala. *Singa keyserlingi* was not found at all and was more or less replaced by the orb-weaver, *Argiope seminola*, which was not encountered at the preceding stand. A total of fifteen species was collected in this series of samples and again the largest part were web-builders. Of the four hunting species all had very low densities.

In order to determine the constancy of the spider population of *Spartina alterniflora* one sample unit was taken from each of ten different stands of this grass. All of this sampling was done during the summer of 1952 except the sample taken in Middle Marshes of Back Sound in 1950. Also the majority of the stands were in estuaries. The location of each stand and the actual counts from each sample are shown in Table 2.

The results of this sampling series again showed *Eustala anastera, Dictyna savanna* and *Grammonota trivittata* making up the major part of the population (Fig. 10). A striking addition to the prevalent species was the jumping spider, *Hyctia pikei*, which had a density surpassed only by Eustala, while at North River and at Station 1 it was present only in very insignificant numbers.

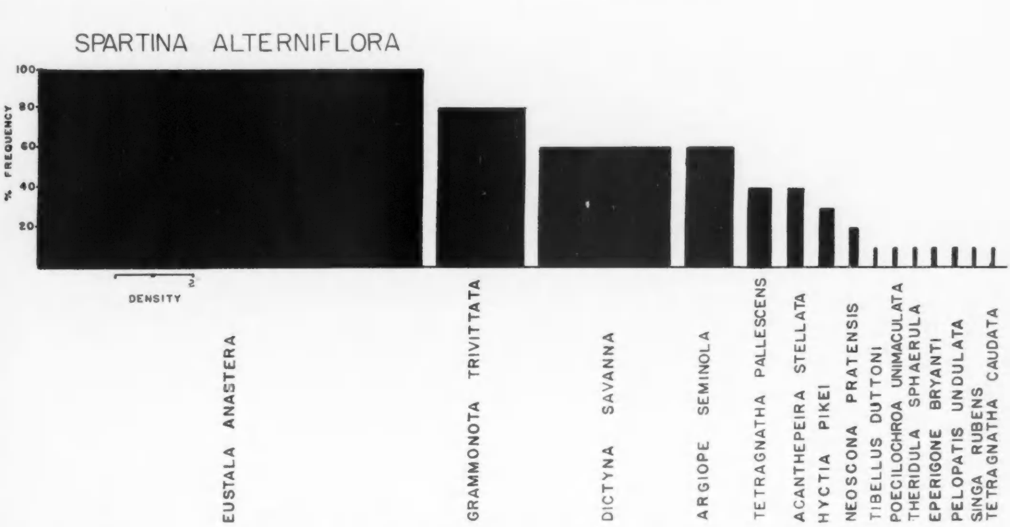

FIG. 9. Frequency-density diagram of the 1952 herbaceous spider population in *Spartina alterniflora* at North River estuary.

TABLE 2. Composition of single sweeping units taken in ten different stands of *Spartina alterniflora*. Estuarian stands are indicated by the letter (E).

	Station 1	Middle Marshes	Town Marsh	Lennox Point	Ward Creek (E)	Harkers Isl. (E)	Harkers Isl. (E)	Williston (E)	North River (E) West Side	North River (E) East Side	CONSTANCY	DENSITY
Grammonota trivittata	3	1	1	1	..	2	..	..	....	3	60%	1.1
Singa keyserlingi	2	..	1	1	..	..	..	..	....	....	30%	.4
Dictyna savanna	2	..	2	1	1	2	..	..	....	5	60%	1.3
Hyctia bina	1	..	..	1	..	..	..	..	....	....	20%	.2
Ceraticelus paschalis	1	..	..	..	..	..	..	..	....	....	10%	.1
Hyctia pikei	..	..	1	1	1	7	3	1	1	3	80%	1.8
Eustala anastera	..	..	3	3	14	3	16	7	3	19	80%	5.8
Tetragnatha pallescens	..	..	..	..	1	..	..	..	3	1	30%	.5
Pelopatis undulata	1	..	..	..	..	..	..	..	....	....	10%	.1
Poecilochroa unimaculata	..	1	..	..	..	..	..	..	....	....	10%	.1
Tetragnatha caudata	..	..	..	1	..	..	..	..	....	....	10%	.1
Neoscona pratensis	..	..	..	..	..	..	1	1	....	....	20%	.2
Argiope seminola	..	..	..	..	..	..	7	..	....	....	10%	.7
Tibellus duttoni	..	..	..	..	..	..	..	1	....	....	10%	.1
Paraphidippus marginatus	..	..	..	..	..	..	..	3	....	....	10%	.3
Total	10	2	8	9	17	14	27	13	7	31	....	12.8

Spartina-Distichlis-Salicornia

Ten sample units taken in this mixed intertidal community from May through June 1952 show a spider population with marked similarities to that of pure *Spartina alterniflora*. Here again *Eustala anastera* and *Dictyna savanna* made up the predominant part of the spider population (Fig. 15). However, *Grammonota trivittata*, which was always found with Eustala and Dictyna in pure Spartina, was completely absent in this community. The other species of spiders collected in this series of samples all had very low densities and were essentially the same as those found in pure *Spartina alterniflora*.

Unfortunately only seven sweeping units were taken in this community in 1951, which is an insufficient number for an accurate interpretation of the density-frequency pattern of the population during that year. Nevertheless, inspection of these sample records showed the same high density for *Eustala anastera* and *Dictyna savanna* as was found in 1952.

When this area was visited in October 1951 the entire community was under water, while during the remainder of the fall, winter, and spring of 1951-52 there was never more than two inches of water over the ground at the time collections were made. It is entirely possible, however, that the October flooding was not the only time in which the vegetation was completely covered by high water, although the winter densities of this community were no lower than those of other maritime communities studied.

During summer the very small amount of flooding which occurs permits this community to support a cursorial population. This ground fauna consisted of only two species, *Lycosa modesta* and *Pardosa floridana*, both wolf spiders. The latter occurred in large numbers; however, flooding and the high water table prohibited the use of pitfall traps for quantitative comparison with other communities. Although most members of the Lycosidae are nocturnal, *Pardosa floridana* was just as active during the day as during the night, and was commonly found running over the wet mud and even submerged beneath tiny puddles of water.

The other member of the ground population, *Lycosa modesta*, was never active during the day and even at night did not extend more than four or five yards out into this zone from the margins of the bordering community of Juncus.

Juncus roemerianus

Ten samples taken in the herbaceous stratum of this marsh rush from June through August 1951 indicated a spider population of very low density. A total of eleven species was collected, all of which were also found in the other intertidal communities; however, in the Juncus community no species made up a predominant part of the population. Although *Eustala anastera* had the greatest density (0.6), it was far too low to be of structural significance. A similar picture of low density was obtained in a series of samples taken in May and June 1952 with *Eustala anastera* and *Neoscona pratensis*, both orb-weavers, slightly predominating (Fig. 15).

The ground fauna of Juncus was exactly the same as the preceding community which it bordered, although *Pardosa floridana* was somewhat less abundant here.

The Juncus community was never subjected to heavy flooding since it was always restricted to the upper part of the intertidal zone.

Uniola paniculata

The sampling carried out in *Uniola paniculata* during May and June 1952 indicated a community of low density and few species in the herbaceous stratum (Fig. 11). Only four species were collected in this series with the long-bodied crab spider, *Tibellus duttoni*, being the most abundant and *Hyctia pikei* ranking second.

Insufficient sweeping samples were taken in 1951 to plot a density-frequency pattern for the population during that year, but essentially the same species were collected with the addition of *Oxysoma cubana*, *Acanthepeira stellata* and *Neoscona pratensis*.

The ground cursorial fauna, as indicated by pitfall sampling, was made up of a number of species with *Trochosa shenandoa* the most abundant (Fig.

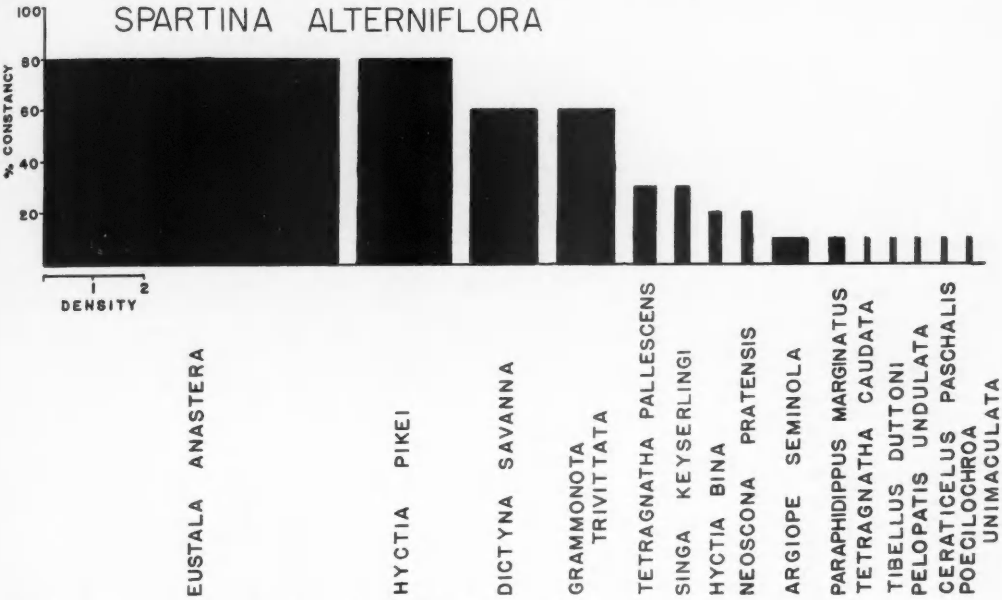

FIG. 10. Constancy-density diagram of the herbaceous spider population in ten different stands of *Spartina alterniflora.*

12). This wolf spider is not as active in summer as in winter when it is mature. During the winter many more specimens were caught in the bases of grass clumps than running over the sand.

As compared to the pitfall samples taken in *Spartina patens,* the ground cursorial fauna had a lower over-all density. Also only three species, *Arctosa littoralis, Trochosa shenandoa* and *Schizocosa salsa,* out of the seven collected in Uniola, were wolf spiders; the others belonged to the cursorial families, Clubionidae, Gnaphosidae, and Salticidae.

Two members of the cursorial population, *Geolycosa pikei* and *Lycosa lenta,* did not appear in the pitfall samples but were taken with a headlight. The Geolycosa are actually sedentary wolf spiders rarely leaving their deep burrows. The males will wander when mature, but the females will go no further than the top of their burrows where they wait for passing prey. The burrows of this species were most common in the shelly, barren area bordering the Uniola and in the banks of the dunes, but a few burrows were found in the sand between clumps of Uniola and one male was taken in a Fieter trap.

Lycosa lenta was not as common here as in other communities but a number of species were taken with a headlight.

Considering the low densities of both the ground and the population living in the upper part of the grass, it was felt that an investigation of the spiders living in the bases of the large clumps of grass might prove worthwhile. The frequency-density pattern of this secretive population based on ten fifteen minute hand samples showed a very large population (Fig. 13). The majority of these species were small and a great many occurred only once or twice in the samples. Three species of this population living among the roots and bases of the grass were very abundant: *Clubiona plumbi, Ariadna bicolor* and *Grammonota sclerata.* Of the twenty-one species collected in these samples thirteen were hunting forms and eight were web-builders. *Grammonota sclerata,* a tiny micryphantid, was the only non-cursorial among the four most abundant species.

Spartina patens

Although the *Spartina patens* community differs from Uniola in the structure of the grass and environmental factors, there appeared to be a marked similarity in the sweeping samples of the two communities. Here again ten sweeping units taken in the herbaceous stratum from June through September 1951 showed a higher density and frequency for the crab spider, *Tibellus duttoni,* than for the other species collected. Although the jumping spider, *Hyctia pikei,* ranked second in abundance, its density was far less than Tibellus and only slightly greater than the ubiquitous orb-weaver, *Eustala anastera.*

A total of six species was collected in this series of samples of which three, *Eustala anastera, Rhomphaea lacerta* and *Dictyna savanna,* were web-builders. In contrast to the intertidal communities, the predominant spiders of the *Spartina patens* community were hunting species. Both *Tibellus duttoni* and Hyctia are long bodied and well abapted for clinging and running on the narrow stems and leaves of *Spartina patens.* It should be pointed out that although *Eustala anastera* was present in this com-

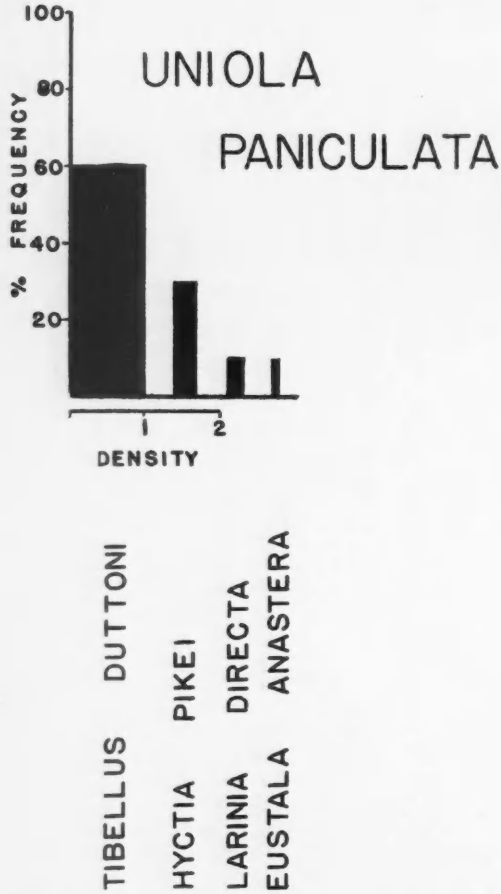

FIG. 11. Frequency-density diagram of the herbaceous spider population in *Uniola paniculata* on Piver's Island.

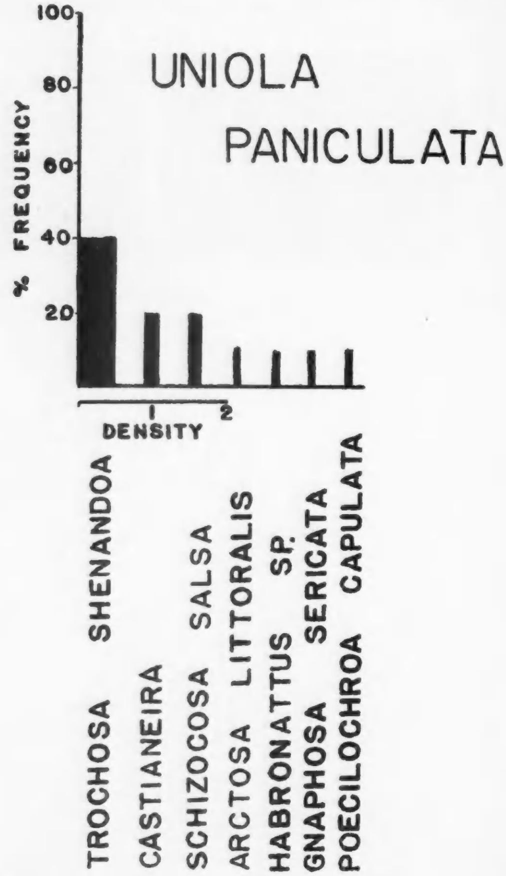

FIG. 12. Frequency-density diagram of the ground cursorial spider population of the *Uniola paniculata* on Piver's Island.

munity, only immature individuals were collected and even these were mostly spiderlings.

The 1952 sweeping samples showed a marked drop in the density of the spider population of this grass (Fig. 16). Particularly striking was the decrease in density of *Tibellus duttoni*, of which only two individuals were collected. The other species, all of which had low densities in the preceding year's samples did not change as markedly, although there was some drop in density. *Dictyna savanna* and *Rhomphaea lacerta* were not collected in the second year's samples while single individuals of three other species, *Larinia directa, Hyctia bina,* and *Argiope seminola,* appeared for the first time.

The ground cursorial fauna of *Spartina patens* was not large but marked by fairly high densities and frequencies of two species, *Lycosa modesta* and *Arctosa furtiva* (Fig. 17). Four additional species, *Gnaphosa sericata, Pardosa floridana, Lycosa rabida* and *Pirata suwaneus,* were taken in this series of pitfall samples during June 1952. Although most of the individuals of *Lycosa modesta* which were taken in these traps were quite immature, night collecting with a headlight and Ficter trap samples during the preceding year also indicated that this was the most abundant of the ground cursorial species in the community. Two other wolf spiders which did not appear in the pitfall samples were taken in random collecting during 1951. These were *Lycosa carrana,* which tended to remain close to the driftline, and several individuals of *Schizocosa salsa.*

The large wolf spider, *Lycosa rabida,* was actually more abundant than the pitfall samples would suggest since the habits of this species tend to minimize the chances of its being taken in the traps. It is only active during the night, at which time it climbs up the stems of the grass waiting for passing insects, and does not ordinarily run over the ground.

Of the eight species which actually composed the ground cursorial fauna in this community only one, *Gnaphosa sericata,* was not a wolf spider. All the others belonged to this family of nocturnal hunters.

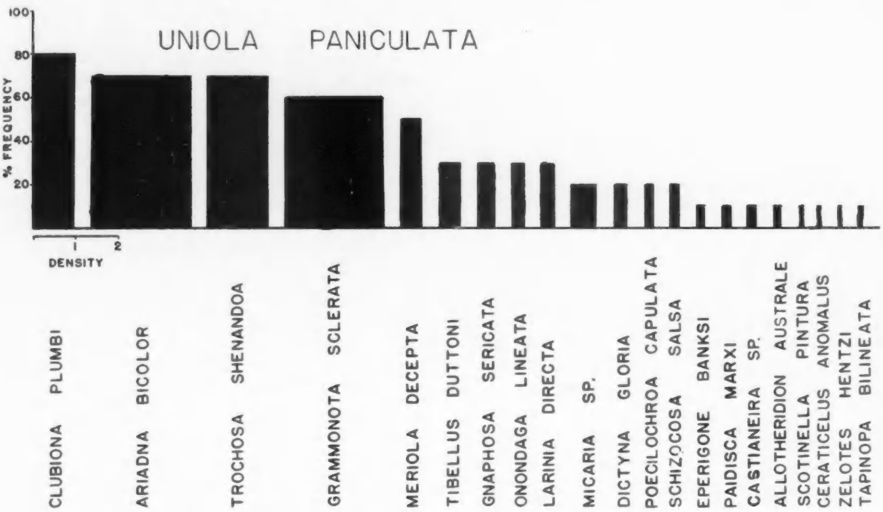

FIG. 13. Frequency-density diagram of the sub-surface spider population in *Uniola paniculata* on Piver's Island.

The few isolated shrubs of Myrica scattered in the *Spartina patens* were not included in the study of this community, but a few random sweeping and beating samples were taken. *Hentzia ambigua* and *Coleosoma normale* were by far the most abundant species. A few specimens of Hentzia appeared in the sweeping samples taken in *Spartina patens*.

Mixed Herbaceous

Ten sweeping units were taken in the herbaceous stratum of a mixed herbaceous community on Carrot Island from June through August 1951. The results of this series of samples showed a fairly large population of eighteen species of spiders living in the vegetation above the ground. A number of species were particularly abundant, although the highest frequency was only 60%. Although the small orb-weaver, *Mangora gibberosa*, had the highest frequency, its density was slightly less than that of the long-bodied jumping spider, *Hyctia pikei*. Two other species, *Latrodectus mactans* and an unknown species of phidippid, had equal densities but were less frequent.

A second series of sweeping samples taken in May and June 1952 confirmed the frequency-density pattern obtained for the population of this community during the preceding year (Fig. 16). *Mangora gibberosa, Hyctia pikei* and the phidippid were again the chief species of the community and although this series of samples showed a marked increase in the density of these three, the relative order remained the same. The black widow dropped to a fraction of its 1951 density and was replaced in position by the orb-weaver, *Neoscona minima*.

Ten pitfall samples were taken during June 1952 and the results showed a ground stratum population of fourteen species with the tiny wolf spider, *Pirata suwaneus*, having the greatest frequency and density (Fig. 17). Here again *Lycosa rabida* was far more abundant than pitfall sampling indicated. It should be pointed out that two species, *Erigone autumnalis* and *Conopistha partita* are web-builders and although collected in pitfall traps, actually do not belong to the ground cursorial population.

Myrica-Ilex-Quercus shrubs

As was mentionad earlier the Myrica-Ilex-Quercus shrub community on Carrot Island represented a younger stage of shrub development exhibiting a somewhat more open condition than that found on the foredunes.

Ten sweeping units were taken in the vegetation of this community from May through June 1952 and a total of seventeen species was collected. The frequency-density pattern resulting from this series of samples formed a complete gradation in density from the most abundant to those species which were quite rare (Fig. 16). Three species, however, made up well over half of the total density of the population. These were in order of density: *Hentzia ambigua, Aysha gracilis,* and *Allotheridion murarium.* Hentzia and Aysha, both hunting spiders, had 100% frequencies and were about equal in density. *Allotheridion murarium,* a small spider which builds irregular webs in the leaves and branches of the shrubs and which belongs to the family of comb-footed spiders, had an 80% frequency and a slightly lower density. In addition to these three species the orb-weaver, *Neoscona minima,* and two species of the crab spider, Xysticus (combined in Fig. 16), were frequently present in the samples.

During the preceding year only beating samples were taken in this community and although a frequency-density diagram could not be drawn from these data, Hentzia, Aysha and *Allotheridion murarium* were by far the most abundant species. Also

all the species, with the exception of *Frontinella communis,* which were collected in 1952, were collected the preceding year. However, one species, *Allotheridion chinda,* which was found a number of times in 1951 did not appear at all in the sweeping samples taken the following year.

Not only was there a heavy population of spiders living in the shrub vegetation above the ground but this community also supported a relatively large ground cursorial population. Ten pitfall samples were taken in June 1952 and a total of twenty-five species was collected (Fig. 17). Following Meioneta, a tiny web-building spider, the six most abundant species in this series of pitfall samples were all cursorial wolf spiders, with *Schizocosa crassipes* having the greatest density and frequency followed by *Pirata suwaneus, Pirata apalacheus, Trochosa abdita* and *Pirata sp.* in that order.

Shrub litter samples were taken continuously from July 1951 through June 1952. Since there is some difference in the thickness and texture of Ilex, Myrica and Quercus litter a unit sample was taken as a combination of the spiders collected in a one square foot sample from each of the three types of shrubs which made up the community. The spiders which live in litter are usually very small and the different species and genera closely resemble each other. Therefore, the frequency-density pattern had to be derived entirely from adult individuals because of the difficulty in placing immatures. However, this modification would have little distorting effect on the over-all picture of the litter population since the important members were found to be continuous breeders.

The total density of the shrub litter population drawn from ten sample units showed one species, *Lathys maculina,* comprising over half the population although eighteen species were collected in all (Fig. 14). Many individuals of this little six-eyed dictynid were found in every sample throughout the year. In addition to *Lathys maculina* two other small species had distinctly greater densities than the remaining species. These were, first, *Lathys albida,* another six-eyed dictynid, and second and slightly less dense, was *Eperigone albula,* a very small micryphantid. Of the remaining fifteen species, all of which had very low densities, only *Neonella vinnula, Meioneta beaufortensis, Erigone autumnalis, Scylaceus pallidus* and *Eperigone maculata* can be considered strictly litter dwellers, and all but *Neonella vinnula* were web-builders. It is somewhat debatable whether to include the other species in the cursorial or in the litter populations. Certainly a sharp line cannot be drawn between these two intracommunity strata.

The three major litter species, *Lathys maculina, Lathys albida* and *Eperigone albula* were collected from all three types of litter but the total population density in each of the three types was quite different. Quercus had the heaviest density of 8.6 adults per square foot sample and a total of fourteen species, while Ilex contained an average of 3.8 adults and seven species. Myrica was somewhat intermediate with 6.3 adults per square foot sample and a total of nine species. The variation in species number was centered around those of very low density which were collected only once or twice and many of which probably should not be considered as belonging to the true litter population.

Persea-Ilex-Quercus Shrubs

Quantitative sampling of the Persea-Ilex-Quercus shrub community on the foredunes of Bogue Bank was carried out in the summer of 1952. The population picture resulting from ten sweeping units taken

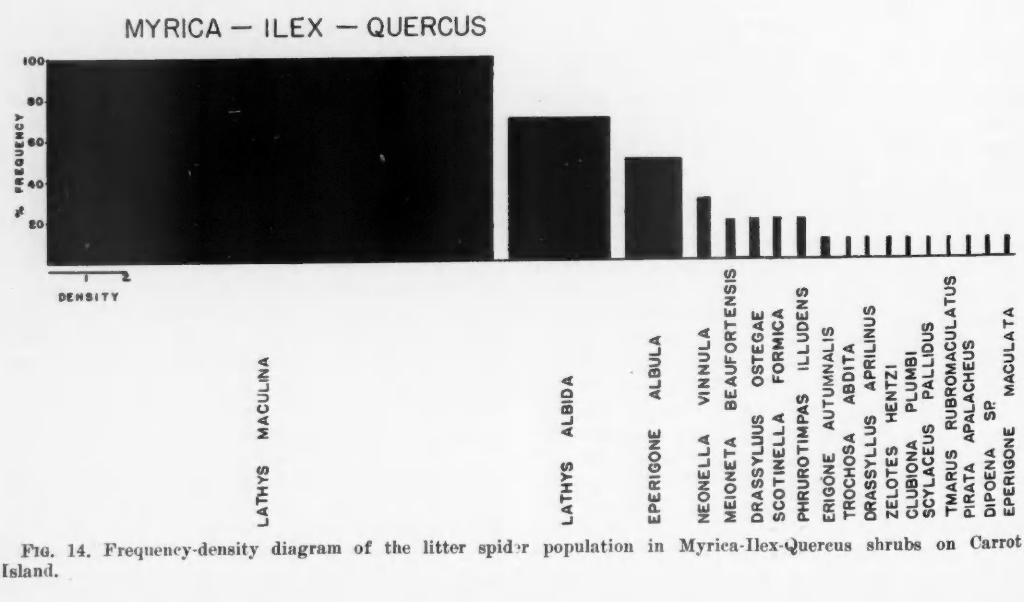

FIG. 14. Frequency-density diagram of the litter spider population in Myrica-Ilex-Quercus shrubs on Carrot Island.

in July showed a density of spiders in the herbaceous stratum which nearly tripled that found in the Myrica-Ilex-Quercus community and was made up of twenty-nine species—eleven more than were found in the other shrub community (Fig. 16).

Four species had 100% frequencies and very high densities. Three were: *Aysha gracilis, Hentzia ambigua* and *Allotheridion murarium,* the same three which made up the major part of the spider population in the Myrica-Ilex-Quercus shrub community. A fourth species, *Grammonota maculata,* which was taken only once in the previously discussed community, here had the highest density of the entire population. The actual difference in the densities of Grammonota, Aysha and Hentzia was very slight, while *Allotheridion murarium* was distinctly smaller.

In addition to these major species quite a few others had rather considerable densities if not 100% frequencies. Three of these, *Conepeira dawsoni, Eustala anastera* and *Epeira pegnia,* were orb-weavers and two, the crab spider, *Tmarus rubromaculatus,* and the jumping spider, *Thiodina iniquies,* were hunting forms. It should also be pointed out that *Anelosimus textrix,* one of the few colonial web-builders, appeared for the first time in this community.

Of the twenty-nine species taken in this series twelve were web-builders and seventeen were hunting forms. Of the four major species of the community, *Grammonota maculata* and *Allotheridion murarium* were web-builders, and *Aysha gracilis* and *Hentzia ambigua* were hunting forms. Only a few beating samples were taken in the vegetation of this community in 1951 but Grammonota, Aysha, Hentzia and *Allotheridion murarium* had the greatest abundance. Two species, *Allotheridion lyricum* and *Euryopis limbata,* were taken once or twice in beating samples but did not appear in 1952.

Despite the fact that the vegetation above the ground supported the heaviest population of all the communities studied, the ground cursorial and litter populations were very low. Ten pitfall samples taken in July 1952 produced a total of thirteen species, but only one, *Phrurotimpas illudens,* had a frequency as high as 40% and a density of 0.4 which is too low for interpretation (Fig. 17). Actually only *Phrurotimpas illudens, Trochosa shenandoa, Habrocestum pulex* and *Schizocosa crassipes* should be considered cursorial. *Conopistha nephilae* and the two species of Xysticus belonged to the stratum above while the remaining species were litter inhabitants.

A number of individuals of the very large cursorial spider, *Dolomedes albineus,* were taken from the sides of the shrub trunks at night. This was the largest species taken in the maritime communities.

Except for *Ancylorrhanis hirsutum,* which appeared for the first time, the same species, *Lathys maculina, Lathys albida* and *Eperigone albula,* were characteristic of the litter samples of this community as in Myrica-Ilex-Quercus. However, the density of the litter population was very low despite the fact that the humus was thick, moist and more homogeneous than in the other shrub community. Ten samples were taken from June 1951 through June 1952 and each square foot sample of litter averaged only 1.6 adults which was less than half of the figure for Ilex in the previous shrub community.

DISCUSSION

Spartina alterniflora: Constancy

The spiders inhabiting the ubiquitous intertidal grass, *Spartina alterniflora,* were the most intensively sampled of all the maritime communities investigated and the resulting sampling data show a population structure that is strikingly constant. This constancy exists not only in regard to the species present in the community but also in the relative densities which each exhibits. Thus, when the results from single sweeping units in ten different stands of the grass are observed, the population structure obtained in terms of frequency and density is essentially the same as that derived from any one concrete stand of the same community.

Sampling in a stand at the mouth of the Newport River estuary over a two year period indicates a similar constancy occurring in time; for although the over all density of the 1952 population was less than that present in 1951, the structural picture of the population had not changed to any significant extent.

It would appear then that just as *Spartina alterniflora* can be projected as an abstract community in a vegetational sense so also does it maintain a very distinct abstract spider population and the variations from stand to stand are probably no greater than that of the vegetation.

Unfortunately this community was the only one in which there was sufficient data taken for a study of constancy in the spider population; but it seems very probable that since the other plant communities included in this study exist in an abstract sense as does Spartina then in parallel manner they too should also support an abstract spider population which would exhibit a constant structure not only in space but also in time. The variations that would occur would probably again be no greater than that found in the vegetation of the same abstract community.

The variation which appears in the abstract spider population of *Spartina alterniflora* is restricted to certain species and is apparently related to the fact that the environmental range of the community is somewhat wider than the range of toleration of the spider species which are present within. This is readily seen by comparing the sampling data taken in a more exposed Spartina stand near the sound to one taken at North River and other stands which are estuarian and thus more protected. A comparison of these data show that in protected estuarian stands the jumping spider, *Hyctia pikei,* and the orb-weaver, *Eustala anastera,* are major members of the community while *Singa keyserlingi* has a low density. In stands of Spartina that are located in or near the sound *Eustala anastera* has a lower density and is represented primarily by immatures and *Hyctia*

pikei is usually absent. The density of *Singa keyserlingi,* on the other hand, increases substantially. The other two major members of this community, *Grammonota trivittata* and *Dictyna savanna,* do not display any noticeable shift in density from estuarian to unprotected stands.

Of the five characteristic spiders in *Spartina alterniflora, Eustala anastera, Hyctia pikei, Grammonota trivittata* and *Dictyna savanna,* the latter three are found, at least in the Beaufort region, only in the intertidal communities; and *Grammonota trivittata* is restricted entirely to the stands of *Spartina alterniflora. Hyctia pikei,* on the other hand, is an important member of several supratidal communities.

Eustala anastera is found in every community although frequently represented by immatures, but shows its greatest density in the maritime communities in *Spartina alterniflora.* This orb-weaver undoubtedly has a wide range geographically; Lowrie (1942) reports it as an important member of the herbaceous and arboreal strata in the black oak community of the Chicago area and Muma & Muma (1949) list it as present, although not abundant, in the mixed grasses and shrub communities of the Nebraska prairie.

The majority of the other species found in this community were rare, that is, had low densities, which probably indicates that the environmental character of the community falls near the outer limits of their range of toleration. The degree to which this is true, and this applies to all species of spiders which had low densities in the other maritime communities studied, can only be ascertained when a large amount of ecological data have been amassed from communities of other areas. It should be pointed out, however, that despite the fact that many of these species are rare in the intertidal communities they are completely absent from all of the other maritime communities. This is true of *Tetragnatha pallescens* and *T. caudata, Pelopatis undulata, Ceraticelus paschalis* and *Theridula sphaerula.*

The Estuarian Intertidal Communities

The three estuarian communities, *Spartina alterniflora,* Spartina-Distichlis-Salicornia, and *Juncus roemerianus,* which compose the extensive salt marshes in the Beaufort area show closely related populations of spiders, the differences being largely a matter of variation in densities. Although all are intertidal, their relationship, as was pointed out in the discussion of maritime vegetation, is distinctly zonational. Juncus extends down from the high tide mark and Spartina occurs along the low tide mark with the mixed community of Spartina-Distichlis-Salicornia forming a middle transitional zone.

Figure 15 shows the 1952 spider population taken in each zone at North River estuary arranged from a corresponding zonational standpoint. It will immediately be seen from this comparison that the greatest population density and number of species occurs in the first zone but drops abruptly with proximity to the high tide mark, with Juncus, the upper zone, having a very sparse population. In all three zones *Eustala anastera* is the most abundant and most frequent species while *Grammonota trivittata* disappears completely in the two communities near the high tide mark. The only species common to all three but more prevalent in Juncus is *Neoscona pratensis.*

The low density in Spartina-Distichlis-Salicornia and Juncus cannot be explained in terms of external environmental factors for they would certainly be no harsher than the lower Spartina zone. A possible explanation might lie in the structure of the vegetation of these communities.

The three plant species which form the middle zone never grow higher than one and one-half feet and are quite widely spaced in contrast to the dense compact zone of pure Spartina which may reach four feet in height. The growth form of this middle zone is undoubtedly correlated with a decrease in hydroperiod. During dry periods in the summer months when the water level of the estuary falls this zone may not be flooded for weeks at a time and the ground becomes dry and baked. The reduction of the spider population is probably a reflection of the reduction in vegetation and the space it affords for webs, etc.

Juncus, on the other hand, which supports the smallest spider population of the three zones, cannot be dismissed in the same manner for it reaches five feet in height and is quite compact. However, the structure of the plant, itself, may be a factor. The stems of Juncus are long, slender and terete, and do not branch. The web-building spiders which rely for web support on the angles produced by branching vegetation would have great difficulty building a stationary web in this type of plant. A web built between two stems would last only a short time in even a mild breeze.

The periodic floodings which these intertidal communities undergo probably do not seriously affect the spider population. When the water level rises several inches above the ground, the wolf spiders present in the ground stratum of the two upper zones undoubtedly move back to higher ground; however, *Pardosa floridana* was found to be active in the mixed zone even when the ground was covered with a half inch of water. The only intertidal community which was ever found completely covered by water was the low Spartina-Distichlis-Salicornia zone. If the spider population was obliterated by this flooding, it could have been easily reformed by the species living in the adjacent Juncus and Spartina zones.

Uniola paniculata

As was mentioned earlier it is difficult to fit the sand-binding Uniola community into the over all picture of maritime vegetation in relationship to the other communities. It is undoubtedly the most xeric of the major maritime communities and its saline hydroperiod is almost non-existent. The exposed white sand surface produces great daily temperature extremes and its invariable location on dunes of different heights makes it more fully exposed to wind

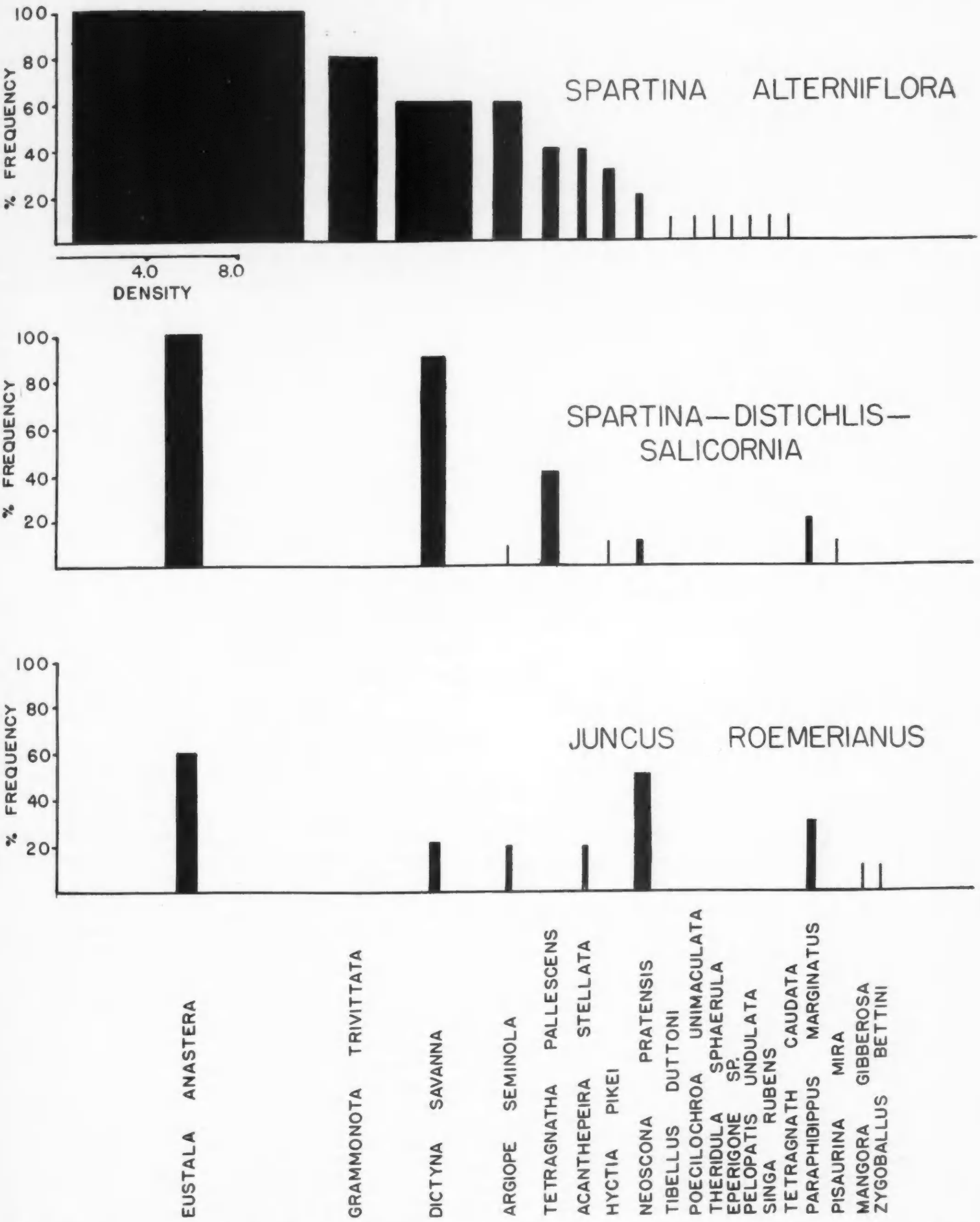

FIG. 15. Frequency-density diagram of the herbaceous spider populations at North River estuary oriented in terms of the zonation of the respective communities.

and radiation than any other maritime community. Only around the roots and the bases of the grass tufts would the extremes of temperature and high evaporation be reduced to less xeric conditions. The structure of the grass provides little in the way toward amelioration of the external environment in the herbaceous and ground level strata.

These conditions are immediately reflected in the spider populations at the three levels. Both the herbaceous and ground levels have very low densities

of spiders and few species. In the herbaceous level *Tibellus duttoni,* which is highly adapted for cursorial activity on grass stems, is the prevalent form. At the ground level the characteristic species is the wolf spider, *Trochosa shenandoa.* This species is nocturnal and thus avoids the high temperatures of the exposed sand surface during the day. Furthermore it is much more cursorial in the winter when it is mature than in the summer. During the latter period it is secretive and hides in the bases of the grass.

In contrast to the population of the two upper strata, that living in the bases of the plants and around the roots is very dense and composed of many species. It should be pointed out that the environment of this stratum can be considered less xeric only in comparison to the upper strata, for the population here, although much greater, is also composed of xeric species. Two of the characteristic species, *Grammonota sclerata* and *Clubiona plumbi,* are also characteristic of the xeric sand beach drift lines (Barnes & Barnes, in press). In those maritime communities which approach mesophytic conditions *Grammonota sclerata* is absent and *Clubiona plumbi* is rare. *Trochosa shenandoa* is probably a less important member of this niche during the winter when it is adult and more cursorial. *Ariadna bicolor,* which is also a characteristic species of this population, is found in the litter of the shrub communities but has a lower density.

Spartina alterniflora, Spartina patens, Mixed Herbaceous and the Shrub Communities: Zonation and Succession

The remaining communities are all members of the maritime zonational series of vegetation which is so characteristic of the coastal area. It will be remembered from the previous discussion that these communities, extending back from the low tide mark, occur in the following order: *Spartina alterniflora, Spartina patens,* mixed herbaceous, Myrica-Ilex-Quercus shrubs, Persea-Ilex-Quercus shrubs and the climax maritime forest. It should be remembered too that the relationship of these communities is not only zonational but also successional.

If the spider population of these communities is now considered in the light of this zonation and its resulting environmental shifts, an understanding of the accompanying shifts of the spider population from one community to the next, as well as the intracommunity relationships, is more readily facilitated. The composite diagrams in Figures 16 and 17 show the results of the 1952 sampling of the spider population in the herbaceous and ground strata reoriented in terms of this vegetational series.

Except for the ground and sub-surface populations of Persea-Ilex-Quercus shrubs, there is in general a steady increase in both the number of species and density in all strata of each community with increasing proximity to the maritime climax.

This general trend is undoubtedly correlated with certain environmental phenomena which have a parallel directional shift. Thus, with increasing proximity to the maritime forest climax there will occur in each community: (1) an increasing modification of the external environment by the plant dominant or dominants, (2) an increasing mesophytic environment, and (3) an increasing degree of stratification.

Considering the herbaceous strata first, in *Spartina alterniflora* there is a population of ten species; however, in the next zone, *Spartina patens,* there is a drop in species number to seven, followed by a sharp rise to nineteen species in the mixed herbaceous zone. In the first shrub community, Myrica-Ilex-Quercus, the species number drops to seventeen but then rises sharply again to twenty-nine in the Persea-Ilex-Quercus community. The slight difference in the species number between the mixed herbaceous and the initial shrub zone is probably due to chance in sampling and is of no real significance. A repeated series of sampling might well show the reverse in species numbers for these two communities. In any case the total number of species contained in each is approximately the same.

The low species number in *Spartina patens,* however, is characteristic and any series of sampling would show a drop in this second zone. This same decrease appeared in the 1951 samples.

The population density of this stratum in each community follows a similar but more even shift. The density in *Spartina alterniflora* was 4.8, *Spartina patens* 1.4, mixed herbaceous 12.1, Myrica-Ilex-Quercus 20, and Persea-Ilex-Quercus 77.3. Here again there is a drop in *Spartina patens.* The low density and number of species of the herbaceous spider population in *Spartina patens* perhaps may be due to a combination of two factors; the herbaceous environment is semi-xeric and the thin slender grass, in contrast to *Spartina alterniflora,* offers much less support for web-building species. The herbaceous population of the *Spartina patens* community is quite similar to the xeric Uniola community.

Not only is there a change in the number and density of species of each community in the series with increasing proximity to the climax community, but there is also a striking shift in the species structure. This change is readily reflected in Figure 16 where it will be noticed that there is a distinct shift to the right as a group of new species appears in each community and certain of those present in the preceding community disappear.

With the exception of *Hyctia pikei* and *Estala anastera* the characteristic species of *Spartina alterniflora* are completely absent in *Spartina patens. Hyctia pikei* and *Tibellus duttoni* become the characteristic species in this latter community. This conclusion is based to some extent on the 1951 samples which show these two species as being by far the most abundant. The radical drop in the density in 1952 is difficult to explain but the relative importance of these species is maintained if the vagrant species, *Hentzia ambigua,* is disregarded. The presence of this species in *Spartina patens* samples is due entirely to the presence of the isolated shrubs of Myrica

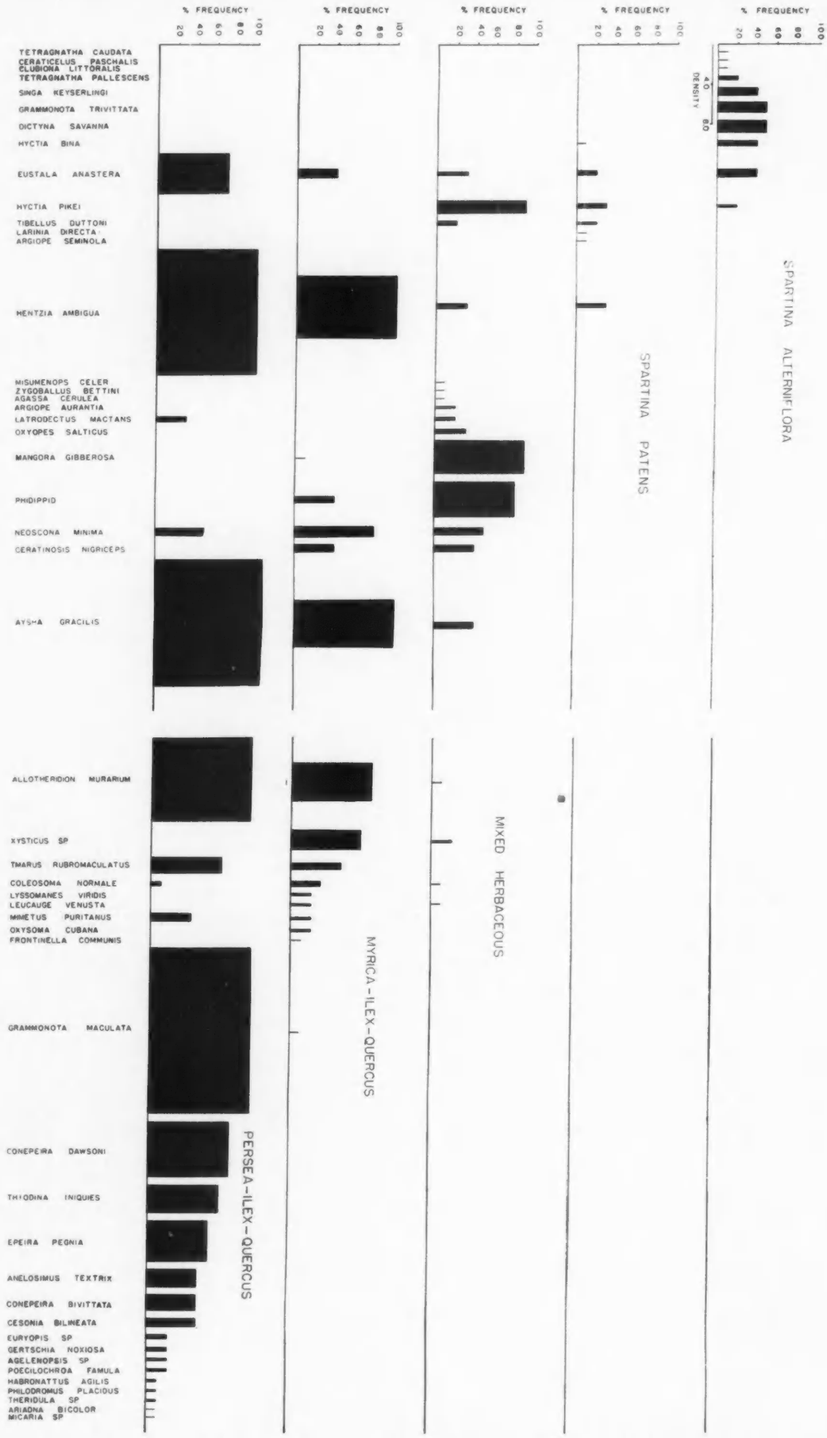

FIG. 16. Frequency-density diagram of the herbaceous spider populations of five maritime communities oriented in terms of their zonation and succession.

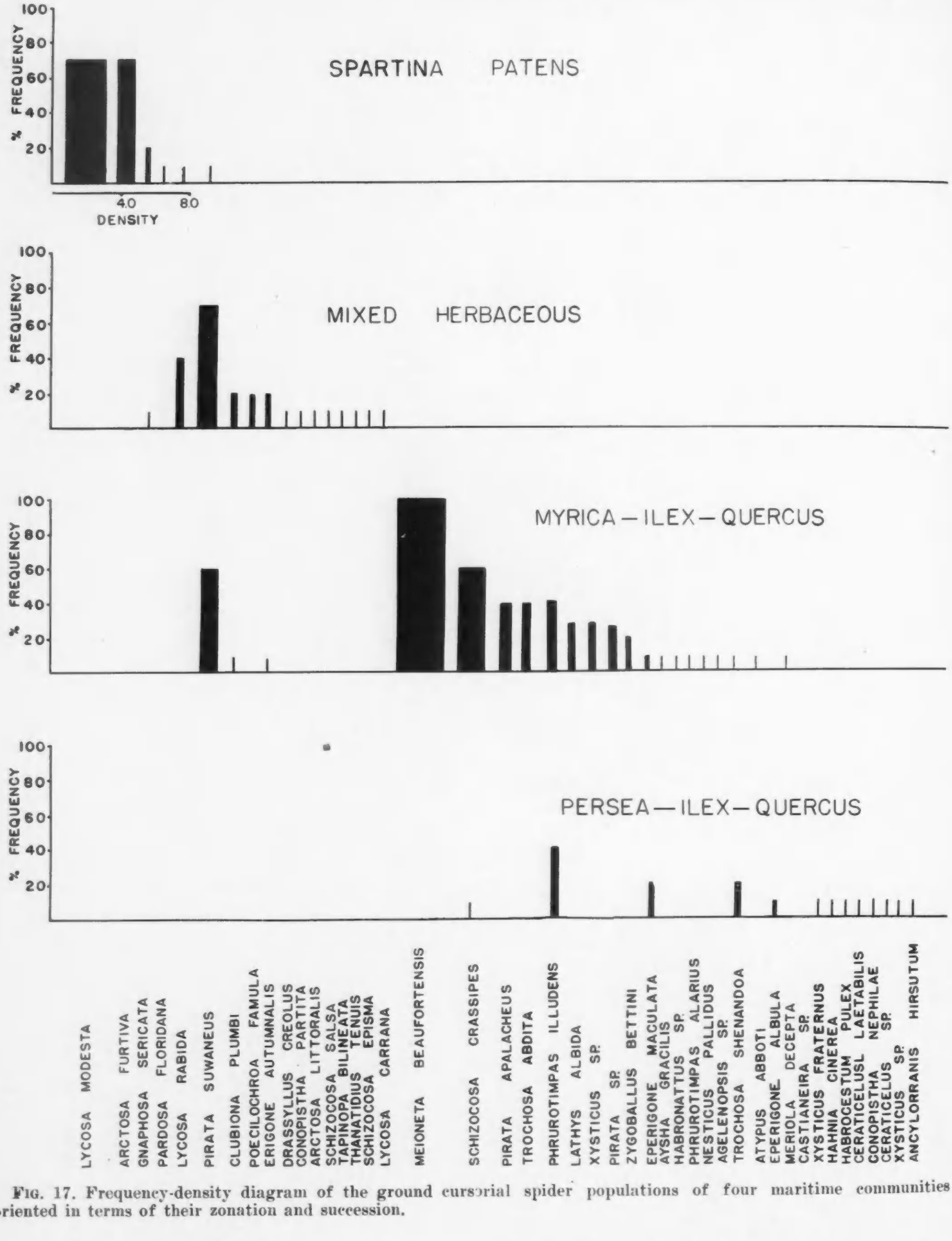

FIG. 17. Frequency-density diagram of the ground cursorial spider populations of four maritime communities oriented in terms of their zonation and succession.

and should not be considered a true member of the *Spartina patens* community.

In the mixed herbaceous community *Hyctia pikei*, along with two other species, *Mangora gibberosa* and an unknown phidippid, continue to maintain an important position.

The greatest shift in population structure occurs in the shrub communities. *Hyctia pikei*, which was characteristic of the preceding herbaceous zone, disappears completely in Myrica-Ilex-Quercus. *Mangora gibberosa* and the phidippid drop sharply in density, while three new species, *Hentzia ambigua*, *Aysha*

gracilis and *Allotheridion murarium* assume dominant positions. These three species maintain their importance in the next shrub zone, Persea-Ilex-Quercus, but are joined by another small web-building form, *Grammonota maculata*.

A characteristic feature of this latter shrub community is the presence of a number of orb-weavers, such as *Conepeira dawsoni*, *Conepeira bivittata* and *Epeira pegnia*, which were not present in the preceding zone. There appears to be a general tendency for the orb-weaving species, particularly the larger forms, to increase in numbers in the more mesophytic communities; this is probably correlated with the increase in space and support afforded for the large webs of these spiders.

From a successional standpoint there is evidence that *Allotheridion murarium* is not the initial major web-builder in the shrubs but rather another theridiid, *Coleosoma normale*. The first shrub to appear following the mixed herbaceous stage is Myrica, which later becomes mixed with Ilex and Quercus. In the few qualitative samples taken in several stands of pure Myrica, *Coleosoma normale* was very abundant and *Allotheridion murarium* was rare. Thus, if *Coleosoma normale* is the initial species, as it appears to be, the succession in shrubs of the characteristic web-building species would run: (1) *Coleosoma normale* in the initial shrubs of Myrica, (2) supplanted by *Allotheridion murarium* in the Myrica-Ilex-Quercus stage and (3) the latter supplanted in abundance, but still holding a major position, by *Grammonota maculata* in the Persea-Ilex-Quercus stage.

The presence of *Mimetus puritanus* in both shrub communities is interesting in that this is a canabalistic species that creeps into the webs of other spiders, killing and feeding on the occupant. This is undoubtedly correlated with the high density of web-building species which serve as food.

In most cases the dominant species of one community are present in the preceding community but in lower density. A number of species, such as *Aysha gracilis*, *Allotheridion murarium* and *Hentzia ambigua*, show a steady numerical increase beginning with the mixed herbaceous community. *Eustala anastera*, however, is the only species present in all five communities.

The relationship of the density of cursorial species to web-builders in the herbaceous strata is roughly equal in the mixed herbaceous and Persea-Ilex-Quercus communities. However, in *Spartina alterniflora* web-building forms compose 82 percent of the total density, while in *Spartina patens* the cursorial species, with a density of 64 percent, make up the greater part of the total abundance. In the Myrica-Ilex-Quercus community the cursorial forms constitute 67 percent of the total density; this is true despite the fact that out of a total of seventeen species making up the population, nine are web-building forms.

Figure 17 shows the pitfall sampling of the ground strata of these communities also reoriented in terms of zonation or succession. The diagram begins with *Spartina patens*, since *Spartina alterniflora* supports no ground fauna, and shows a steady increase in the number of species in the mixed herbaceous and Myrica-Ilex-Quercus community. Density follows a somewhat similar pattern although *Spartina patens* and the mixed herbaceous communities were about equal. This is probably somewhat misleading for the latter community would show a distinct increase in density over *Spartina patens* if *Lycosa rabida* was represented in the pitfall samples in numbers more equivalent to its actual abundance. As has already been mentioned the habits of this species will not allow accurate sampling of its density by the pitfall method.

Except for *Meioneta beaufortensis*, all of the most abundant species in the Myrica-Ilex-Quercus zone are wolf spiders. In *Spartina patens*, *Lycosa modesta* and *Arctosa furtiva* are the characteristic spiders. These two wolf spiders disappear completely in the mixed herbaceous community and are supplanted by *Lycosa rabida* and *Pirata suwaneus*; both of these species are present but rare in *Spartina patens*. In the Myrica-Ilex-Quercus shrubs *Lycosa rabida* disappears while *Pirata suwaneus* maintains an important position, but is overshadowed in abundance by Meioneta and *Schizocosa crassipes*. Meioneta is not a wolf spider and it does not belong to a cursorial family; nevertheless this species must be an active wanderer in order to be taken so frequently in pitfall traps. It was rarely found in Berlese funnel samples.

The low density and numbers of species of the ground fauna of Persea-Ilex-Quercus shrubs is unexplainable particularly in view of the very large population of spiders which the herbaceous stratum exhibits. The environmental conditions are certainly more mesophytic, if anything, than those of the Myrica stage and there is a much heavier deposition of litter in the Persea community. Whatever the factor is that reduces the ground population of this particular stand, it may not be typical for the abstract community.

The litter populations of the two shrub communities were the most intensively studied. The litter of *Spartina patens* and the mixed herbaceous communities was too thin and too sparse for adequate quantitative samples; the few qualitative samples taken indicated a very low population and contained mostly cursorial species.

The environmental conditions of this particular stratum, from the successional and zonational standpoint, show marked changes. There is a gradual increase in the thickness of the litter which would therefore result in a higher moisture content of the soil and litter in each community as the mesophytic maritime forest climax is approached. The alkaline condition of the initial saline soils would also decrease with the gradual accumulation of litter in the course of succession.

The Persea-Ilex-Quercus community, even though it had a very thick and homogeneous litter, maintained a very low population of spiders in comparison to

Myrica-Ilex-Quercus. This, like the low density of the ground cursorial population, is surprising and unexplainable.

The spider population of the Persea-Ilex-Quercus community, particularly of the herbaceous stratum, is undoubtedly close to the population of the climax maritime forest. Random collections made by the author in 1950 in the live oak forest on Shackleford Bank demonstrated that all of the major species of the shrub communities were represented there. These two shrub communities might well be considered to have a sub-climax population of spiders.

This maritime succession and zonation of spiders agrees very closely to the results of Lowrie's study (1948) of the zonation and succession on Lake Michigan dunes. The successional series of communities with which he was concerned were: beach, foredune grasses, cottonwoods, black oak, sub-climax forest and the beech-maple climax forest. He found the greatest density and number of species in the black oak community rather than in the climax. The ground-litter population of the beech-maple climax was only one-half of that found in the black oak stage.

Seasonal Succession of Spiders

Both Elliot (1930) and Muma & Muma (1949) were concerned with the seasonal changes in the communities which they studied and both found population peaks in late spring and early fall. Although seasonal aspects of the maritime communities were not studied, such population peaks also undoubtedly occur here but it is doubtful if they would radically alter the frequency-density patterns taken at different times in late spring, summer and early fall. The immatures of a species are always more abundant than the adults, which could slightly change the density of that species if all sampling were carried out at one time; but even if a certain species has a peak in late spring, it will not be rare in the same community in the fall. Elliot described a seasonal succession of spiders on the forest floor of the beech-maple forest. Such a succession might well have occurred if he had been concerned only with adults, but it is highly unlikely that such a succession would have existed if he had placed all immatures collected in his sampling.

Although all intensive sampling and the compilation of community structure in this study was restricted to late spring, summer and early fall, collections were made in the winter. From the over-all sampling the spider populations of the maritime communities were found to have an essentially constant structure from late April through October with minor fluctuations due to maturation and breeding. With the onset of the first freezing temperatures in November the densities of the herbaceous and ground cursorial strata, particularly the former, dropped sharply. The litter population, however, remained constant throughout the winter except for vagrants from the other strata. At the end of March the densities of the upper strata began to increase and by the last of April the summer structure had been essentially reassumed.

SUMMARY

1. The variation in the saline water table is probably the primary factor determining the formation of the major maritime plant communities and the zonational and successional series in which they occur. On the coast of North Carolina the zonation and succession of vegetation consists of the following series of communities beginning in the intertidal zone and ending in the climax maritime forest: *Spartina alterniflora*, *Spartina patens*, mixed herbaceous, Myrica-Ilex-Quercus shrubs, Persea-Ilex-Quercus shrubs and the maritime live oak forest. Also characteristic of the coastal area are the estuarian *Juncus*

TABLE 3. Summary of the population structure of the major maritime communities at Beaufort, N. C.

Community and Stratum	Density	Total No. Sp.	Characteristic Species
Spartina alterniflora			
Herbaceous......	moderate	22	*Grammonota trivittata, Dictyna savanna, Eustala anastera, Hyctia pikei*
Ground.........	none	none	
Sub-surface......	none	none	
Spartina-Distichlis-Salicornia			
Herbaceous......	moderate	8	*Dictyna savanna, Eustala anastera, Hyctia pikei*
Ground.........	moderate	2	*Lycosa modesta, Pardosa floridana*
Sub-surface......	none	none	
Juncus roemerianus			
Herbaceous......	very low	12	*Eustala anastera, Neoscona pratensis*
Ground.........	moderate	2	*Lycosa modesta, Pardosa floridana*
Sub-surface......	none	none	
Uniola paniculata			
Herbaceous......	low	6	*Tibellus duttoni, Hyctia pikei*
Ground.........	low	9	*Trochosa shenandoa, Lycosa lenta*
Sub-surface......	high	21	*Clubiona plumbi, Grammonota sclerata, Ariadna bicolor*
Spartina patens			
Herbaceous......	low	8	*Tibellus duttoni, Hyctia pikei*
Ground.........	moderate	8	*Lycosa modesta, Arctosa furtiva*
Sub-surface......	low	..	Largely cursorial
Mixed Herbaceous			
Herbaceous......	moderate	22	*Mangora gibberosa, Hyctia pikei Phidippid*
Ground.........	moderate	14	*Pirata suwaneus, Lycosa rabida*
Sub-surface......	low	..	Largely cursorial species
Myrica-Ilex-Quercus			
Herbaceous......	high	20	*Aysha gracilis, Hentzia ambigua, Allotheridion murarium*
Ground.........	high	24	*Meioneta beaufortensis, Schizocosa crassipes, Pirata suwaneus*
Sub-surface......	high	18	*Lathys maculina, Lathys albida, Eperigone albula*
Persea-Ilex-Quercus			
Herbaceous......	high	30	*Grammonota maculata, Aysha gracilis Hentzia ambigua, Allotheridion murarium*
Ground.........	low	13	Not distinct
Sub-surface......	low	7	*Lathys maculina, Lathys albida, Eperigone albula, Ancylorrhanis hirsutum*

roemerianus and Spartina-Distichlis-Salicornia communities as well as the dune grass *Uniola paniculata.*

2. The structure of the spider populations was determined for each of these communities with the exception of the forest climax. The investigation was carried out at Beaufort, N. C. during 1951 and 1952.

3. A total of 139 species of spiders belonging to 24 families were collected in the maritime communities.

4. Each community displays a distinct population structure of spiders characterized both by the presence of certain species and by the relative density which each exhibits.

5. Sampling in ten different stands of *Spartina alterniflora* and in one stand over a two year period indicates that the population structure of spiders living in this community exhibit a constancy not only in space but also in time. Thus, the abstract *Spartina alterniflora* community supports an abstract spider population which is essentially the same as that in any one concrete stand.

6. The three estuarian intertidal communities which occur in distinct zones support closely related spider populations but the structure which each exhibits is sharply different.

7. The dune community of Uniola is the most xeric of the maritime communities. This environment is reflected in the xeric species of spiders which the community supports, many of which are also characteristic species of the dry sand beach drift lines.

8. The zonation and succession of maritime vegetation produces a zonation and succession of spiders beginning in the intertidal communities and ending in the maritime forest. This succession, in general, is characterized by an increasing number of species and population density with proximity to the maritime climax. This may in turn be correlated with the increase in stratification of the intracommunity environment and the greater number of ecological niches afforded by the vegetation.

9. Table 3 summarizes the spider population characteristic of each of the maritime communities investigated.

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FACTORS DETERMINING THE ROLE OF LOBLOLLY PINE AND SWEETGUM IN EARLY OLD-FIELD SUCCESSION IN THE PIEDMONT OF NORTH CAROLINA

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INTRODUCTION

Secondary succession on upland old-fields in the Piedmont of the southeastern United States has been the subject of several investigations.

Crafton & Wells (1934) traced the earliest stages of succession on abandoned fields. Billings (1938) and Coile (1940) dealt with the vegetational and soil changes that occur during the development and decline of shortleaf and loblolly pine forests. Oosting (1942) followed succession from the abandoned field to the climax forest. Barrett & Downs (1943) made quantitative studies of the rate of hardwood invasion into pine stands under different conditions.

According to Oosting, succession generally tends to proceed as follows: fields that are abandoned one year are dominated by *Leptilon canadense* and *Digitaria sanguinalis*. *Aster ericoides* assumes dominance during the second year, usually being mixed with *Ambrosia artemisifolia*. By the third year, *Andropogon* sp. generally becomes dominant and remains so until it is shaded out by invading pines (*Pinus taeda* and *P. echinata*). Generally, pine invasion begins within 5 years following abandonment, and a closed stand may be formed within 10 to 15 years. Once stand closure takes place, pine is unable to perpetuate itself in its own shade; however, several hardwood species are able to invade pine stands. As a consequence, a middle-aged (40-year) pine stand will have a distinct understory of hardwoods. Pines 75 years of age are apt to be overmature, and as they thin out they are replaced by hardwoods which have steadily increased in the lower strata. Eventually (150 to 200 years) hardwood dominance (principally oaks and hickories) will be attained with scattered pines remaining as relicts.

THE PROBLEM

The problem of why pine fails to reproduce under pine has received much attention (Coile 1937, 1940; Billings 1938; Korstian & Coile 1938; Reed 1939; Oosting & Kramer 1946; Kozlowski 1949; etc.), though another important phase of succession has been almost wholly neglected. This phase is concerned with reasons why pine gains dominance in the first place, or why hardwoods do not more frequently enter and dominate the first arboreal stage of upland old-field succession.

In general, there are two broad points of view on this subject. The first attributes pine dominance to the mobility of its seed and/or to the preponderance of pine seed sources. Supporting this view, Billings (1938) stated that pine invaded old-fields due to the wind-borne nature of its seed. Coile (1940) later suggested that invasion of old-fields was determined, for both pine and hardwood, by the abundance of seed produced, weather conditions, and the

* Contribution from the Department of Botany, Duke University, Durham, N. C.

size of the field. Another view is that pines, rather than hardwoods, invade most abandoned fields because of their superior adaptability to old-field conditions.

To evaluate these points of view, studies were made on the relative importance of seed source and specific adaptability to old-field conditions as factors determining the role of pine and hardwood species in early old-field succession.

Due to the very broad nature of this problem and to the large number of species that could be involved in the invasion of old-fields, it was impractical to attempt a general study. Rather, it was thought more information could be gained by concentrating on a study of two species, one pine and one hardwood, both of which seemed fitted to fill the role of the first arboreal dominant in old-field succession.

Pinus taeda L. was chosen as the pine species because it is one of the more common old-field trees in this region.

The hardwood species was selected on the basis of its estimated potential for invading old-fields. In general, it was thought that it should have the following characteristics:

(1) Ability to grow into a large tree.

(2) Wind-borne seed.

(3) Wide ecological amplitude, i.e., it should be found growing under a wide range of ecological conditions, particularly on upland sites in this region.

Liquidambar styraciflua L. was chosen because it appeared to meet these qualifications better than any other local hardwood tree species.

It is fast growing and capable of reaching heights of 150 ft. and diameters up to 5 ft. Ordinarily, however, at its best it attains heights of 80 to 120 ft. and diameters of 3 to 4 ft.

Its seeds are much smaller than those of loblolly pine. A pound of uncleaned seed contains between 65,000 and 90,000 seeds, while a pound of cleaned loblolly pine contains only 16,000 to 25,000 seeds (Anon. 1948). Furthermore, the light sweetgum seed has a small wing, consequently it seems particularly adapted to wind distribution.

The extensive range of the tree gives some indication of its ecological amplitude. In southern Connecticut it forms part of a willow oak-sweetgum-persimmon forest (Bray 1930). From there it spreads southward along the Coastal Plain and Piedmont to Texas and throughout the lower Mississippi and Ohio river valleys. It is also found growing in dense stands in Mexico (Miranda & Sharp 1950).

In Virginia and the Carolinas it is very common (Cruikshank & Roberts 1941a, 1941b; Evans 1942). In the North Carolina Piedmont, sweetgum attains its greatest density east of Caswell, Alamance, and Chatham counties. There it forms one of the most important components of the upland loblolly pine-hardwood forest type (Cruikshank 1940).

Plan of Study

It was thought that the most pertinent information could be gained by a systematic comparison of the two species during various times in their life histories. Of necessity, such comparisons were limited in scope, but it was hoped that they would lead to generalizations on the main problem and indicate profitable areas for more intensive research.

The following experimental and observational comparisons were made and the results are presented under the indicated sections:

Section I. The photosynthetic fitness of loblolly pine and sweetgum for growth under old-field conditions.

Section II. Observations on the occurrence of loblolly pine and sweetgum reproduction in abandoned fields, and on the factors affecting their respective distributions.

Section III. An experimental comparison of the effects of drying on germinating seeds of both species.

Section IV. Experimental and observational data on the relative survival of seedlings of both species under field and laboratory conditions.

Section V. Field observations on the relative growth of both species under old-field conditions.

Field observations were also made on the relative abundance of seed sources of both species, and on the factors contributing to their development. These will be found in the general discussion.

It is a pleasure to acknowledge the assistance received from members of the Botany Department and School of Forestry of Duke University. Particularly, I would like to express my sincere thanks to Professor H. J. Oosting for his advice; to Professors T. S. Coile and P. J. Kramer for help with the soil and physiological phases of the work; and to Professor F. X. Schumacher for his direction of the statistical aspects of the problem.

SECTION I. PHOTOSYNTHETIC FITNESS TO GROW UNDER OLD-FIELD CONDITIONS

Much work has been done on the photosynthesis of loblolly pine (Decker 1944; Kramer & Decker 1944; Kozlowski 1949). In general, it has been found that this species is well suited to the light and soil moisture conditions that usually prevail on most abandoned fields. It attains its maximum photosynthetic rates in full sunlight and, apparently, so long as it receives adequate sunlight it is able to compete successfully for soil moisture.

In contrast, little is known of the light and soil moisture requirements for the growth of sweetgum. Trenk (1929) stated that sweetgum makes its best growth in full sunlight but that it will persist in heavy shade for years. Chittenden (1906) claims that throughout its entire life it is intolerant of shade. In seeming opposition to Chittenden's view is the fact that sweetgum on the uplands of this region is found growing mainly in the shade of pine and rarely in the full sunlight of old-fields.

To obtain data on the growth requirements of sweetgum three experiments were performed using 3-year-old sweetgum seedlings. The first measured apparent photosynthesis at various light intensities. The second tested the effects of continuous illumination at two different light intensities on the total daily photosynthesis. The third measured apparent photosynthesis under various conditions of soil moisture at full light intensity.

Parts of these data were used to evaluate, in terms of light intensity, the suitability of the abandoned field for the growth of sweetgum seedlings. Other data were used to compare the photosynthesis of seedlings of both species under conditions of moisture stress (the loblolly pine data are from Kozlowski, 1949).

All of the experiments were conducted by using the Decker (1944) photosynthetic apparatus. The operation of this equipment is based on the measurement of carbon dioxide absorption by plants placed in chambers under controlled conditions of air flow, light, and temperature. Decker (1944) described the earlier-used apparatus, which was slightly modified by Kozlowski (1949). As used here, the absorption towers were replaced with a Grubb-Parson Infrared Gas Analyzer.

General Technique Used in Photosynthesis Experiments

The potted plants were kept in one of the cooler, shaded rooms of the greenhouse. When they were brought out they were placed directly in the apparatus. Under these conditions they were never subjected to full sunlight or temperature extremes prior to the measurement of their apparent photosynthesis. This procedure eliminated the possibility that plants, kept in full sunlight, would have been subject to different types of preconditioning prior to testing, e.g., full sunlight and high temperatures on sunny days and shade and relatively lower temperatures on cloudy days.

All plants, prior to testing, were given one-half hour to become adjusted to light and temperature conditions in the plant chambers. Kozlowski (1949) had found this length of time sufficient for overcup oak seedlings to become adjusted to a light change from 2300 to 9500 foot candles.

Light was varied through the use of screens made with cheese-cloth, screen wire, etc. Its intensity was determined by an average of 9 readings made with a Weston Illuminometer held 1 in. below the top of each plant chamber.

The temperatures within the chambers were controlled by the air and water cooling systems described in the earlier papers. Temperatures were maintained at 25 ± 1.5°C.

The rate of air flow was maintained so that the concentration of Co_2 in the air leaving the chambers was approximately 15% below that of free air. Both Heinicke & Hoffman (1933) and Decker (1944) had found that photosynthesis was not retarded when about 15% of the atmospheric CO_2 was removed.

The data collected were expressed in two ways: mg of CO_2 absorbed per minute (1) per gm of oven dry weight of foliage and (2) per 100 sq cm of stomated leaf surface. Since it was found that results based on leaf area were comparable to those based on leaf weight, only leaf area results are presented. All data and statistical analyses not presented in the text are on file in the Duke University library.

Leaf area was obtained by the photoelectric method in an apparatus described by Kramer (1937).

Experiment 1. The Apparent Photosynthesis of Sweetgum Seedlings at Various Light Intensities with Soil Moisture at Field Capacity

METHOD

Six 3-year-old sweetgum seedlings were used in this experiment. Previously they had grown in clay pots out of doors in full sunlight. Each seedling was transplanted into a 5-quart oil can containing a known weight of greenhouse loam at field capacity. Soil moisture in each can was maintained at field capacity by adding an amount of water, each evening, equivalent to that lost during the day. About 6 weeks were allowed for the roots to become adjusted to the new environment.

During a period of 6 days in August, 1950, the apparent photosynthesis of these plants was experimentally measured under 6 different light intensities (300, 1450, 2900, 5290, 7200, and 10,000 foot candles). A random block experimental design was employed in which three runs of two plants each were completed each morning, with a new light intensity being used each day. Each plant appeared in each run twice and at each light intensity once. Prior to each run, the plants were randomly assigned to the chambers.

RESULTS AND DISCUSSION

Statistical analysis of the data showed that there was a significant difference between treatments and plants. Statistical tests indicated that there were no significant differences (5% level) between the means at 2900, 5290, 7450, and 10,000 f.c. There were highly significant differences (1% level) between all these means and the means at 1450 f.c. and 300 f.c. The mean at 1450 f.c. was significantly different (1% level) from the mean at 300 f.c.

Sweetgum reaches its near maximum photosynthesis between 1450 f.c. and 2900 f.c. (Fig. 1). Kramer & Decker (1944) and Kozlowski (1949), working with other species of hardwoods common to the uplands of this region, obtained similar results.

These data are at obvious variance with Chittenden's (1906) statement that sweetgum is intolerant to shade throughout its entire life. Probably its failure to reproduce heavily in some shaded situations (e.g., upland oak-hickory forests and well-developed bottomland forests) results from causes other than intolerance to shade.

As noted above, there was no significant difference

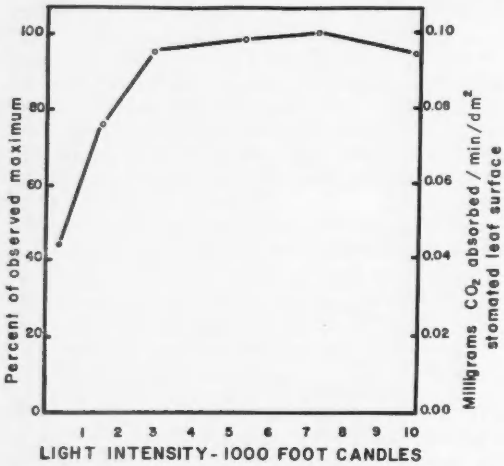

FIG. 1. Effect of light intensity on apparent photosynthesis of sweetgum seedlings. Each point represents the mean of six observations.

in apparent photosynthesis under conditions of full light or limited shade (Fig. 1). Thus, in terms of light intensity, it appears that both the abandoned field and the floor of young pine forests are suitable for the growth of sweetgum. Further consideration will be given to this phase of the problem in experiment 2.

EXPERIMENT 2. THE APPARENT PHOTOSYNTHESIS OF SWEETGUM SEEDLINGS UNDER CONTINUOUS ILLUMINATION AT TWO DIFFERENT LIGHT INTENSITIES

It was indicated in experiment 1 that there was no significant difference between apparent photosynthesis at 2900 f.c. and 10,000 f.c. However, since these measurements were made during one period of the day between 9:00 A.M. and 12:00 A.M., they indicate nothing of the overall daily photosynthesis. It is possible that under conditions of continuous illumination, the total apparent photosynthesis at one of these light levels would statistically exceed the total at the other light level (Nutman 1937).

Experiment 2 was devised to get information on the total daily rate of apparent photosynthesis under continuous illumination at 3200 f.c. and 10,000 f.c. The first light level was chosen because it was near the lower limit for maximum photosynthesis as indicated by experiment 1 and also because it approximated the light intensity found under a 31-year-old loblolly pine stand by Korstian & Coile (1938). The second light level was chosen because it approximated light levels found in the old-fields.

METHOD

The six plants used in experiment 1 were again employed here. Each plant was subjected once to continuous illumination (8 A.M. to 4 P.M.) at each intensity. The different light intensities were used on alternating days because difficulties of temperature regulation made it impossible to use both intensities at once. Readings of apparent photosynthesis were made hourly.

Soil moisture was maintained at field capacity as in experiment 1. The temperature was held at $25.5 \pm 1.5°C$.

RESULTS AND DISCUSSION

Apparent photosynthesis under continuous illumination at 10,000 f.c. reached a maximum in the early morning, thereafter it declined at a fairly uniform rate (Fig. 2). Under continuous illumination at 3200 f.c. a maximum was reached in the mid-morning. This was followed by an erratic decline. In general, after eleven o'clock the rate at 3200 f.c. tended to exceed the rate at 10,000 f.c.

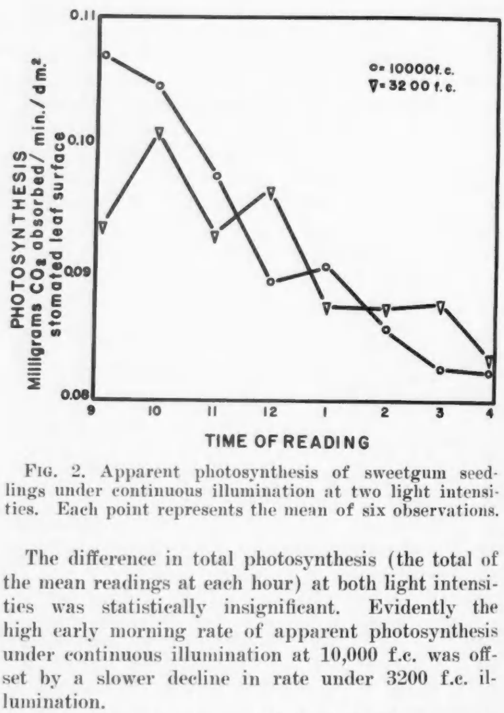

FIG. 2. Apparent photosynthesis of sweetgum seedlings under continuous illumination at two light intensities. Each point represents the mean of six observations.

The difference in total photosynthesis (the total of the mean readings at each hour) at both light intensities was statistically insignificant. Evidently the high early morning rate of apparent photosynthesis under continuous illumination at 10,000 f.c. was offset by a slower decline in rate under 3200 f.c. illumination.

These data indicate, as did the data from experiment 1, that sweetgum seedlings are tolerant to limited shade or to full sunlight. It may be concluded on the basis of experiments 1 and 2 that, in terms of light intensity, both the old-field and the pine forest would make favorable habitats for the growth of sweetgum.

EXPERIMENT 3. THE APPARENT PHOTOSYNTHESIS OF SWEETGUM SEEDLINGS UNDER VARIOUS SOIL MOISTURE CONDITIONS AND FULL LIGHT INTENSITY

Experiment 3 was designed to give information on the apparent photosynthesis of sweetgum seedlings under full light intensity and various soil moisture conditions. Kozlowski (1949) showed that the ap-

parent photosynthesis of loblolly pine decreased rapidly as soil moisture stress increased. The objective of this experiment was to duplicate, as nearly as possible, Kozlowski's work in order to obtain comparable data. It was hoped that a comparison of these data would give an indication of the relative suitability of each species for growth under conditions of soil moisture stress, particularly in mixed stands after stand-closure takes place and competition for soil moisture develops.

METHOD

Six 3-year-old potted plants were used in this experiment. Each plant was transplanted into a 5-quart oil can containing a known weight of air dry soil with a wilting percentage of 3.1 and a field capacity of 18.9 (determined after one day of free drainage). This soil was similar to that used by Kozlowski (1949). The plants were allowed 6 weeks for their roots to become adjusted to their new environment.

Soil moisture in each can could be estimated by weighing, since the weight of the can and the weight of the soil at field capacity and at the wilting point were known. All water losses from the soil were due to transpiration, since evaporation from the cans was prevented by the use of double oilcloth covers.

The experiment was performed over a period of 15 days during July and August, 1950. Apparent photosynthesis was measured at field capacity and then the soil was allowed to dry, thereafter measurements were made at convenient intervals. Six levels of soil moisture were employed; however, at any one level there were slight differences between cans, since the soil in different cans did not dry at the same rate.

Three runs of two plants each were completed during the afternoons when measurements were taken. Each plant appeared at each moisture level once and in each run twice. The plants were randomly assigned to the chambers before each run.

RESULTS AND DISCUSSION

The results indicate that photosynthesis declined slowly at first, and then rapidly as the availability of soil moisture decreased. In this respect they are in accord with the findings of Schneider & Childers (1941), Loustalot (1945), and Kozlowski (1949).

The data were subjected to regression analysis. The regression equation was of the same form as that used by Kozlowski in the analysis of his loblolly pine data:

$$Y = a + b_1X_1 + b_2X_2$$

where, for any seedling, Y=percent maximum photosynthesis, $X_1=100$ divided by the percent of soil moisture at the time of the determination of the photosynthetic rate, and $X_2 = (X_1)^2$. Numerical equivalents were calculated for the variables and for the constants. The final equation was

$$Y = 106.9326 - 1.7523\ (X_1) - 0.0853\ (X_2)$$

The reciprocal curve for this equation is presented in Fig. 3 along with the curve for loblolly pine calculated by Kozlowski (1949). A comparison of these curves seems justified since both experiments were performed under similar conditions using the same apparatus.

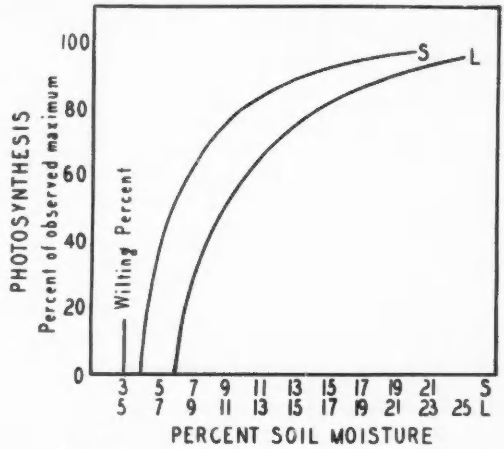

FIG. 3. Apparent photosynthesis of loblolly pine (L) and sweetgum (S) in full light, 10,000 foot candles, under various conditions of soil moisture. Loblolly pine data from Kozlowski (1949).

A comparison of the two curves indicates that the decline in photosynthesis with increasing soil moisture stress is very similar for both species. However, it appears that sweetgum is able to maintain a higher percentage of maximum photosynthesis under almost all conditions of moisture stress below field capacity, particularly near the wilting percentage. As a consequence, it is probable that after stand closure takes place and competition for soil moisture develops, the photosynthetic rate of sweetgum, in relation to pine, would not be disproportionally reduced.

SECTION II. OBSERVATIONS ON THE OCCURRENCE OF SWEETGUM AND PINE REPRODUCTION ON ABANDONED FIELDS

Many observations were made of abandoned fields, during 1950 and 1951, in an effort to determine the relative abundance and distribution of loblolly pine and sweetgum reproduction and in the hope that indications of controlling factors might be noted.

Pine reproduction was prominent on almost all of the abandoned fields visited. From this it was concluded that pine was capable of becoming established, in considerable numbers, on almost any abandoned upland site. It appeared that the density of its reproduction would be influenced by various factors including seed source, site, and weather conditions; but the importance of the individual factors could not be determined.

Occasional sweetgum seedlings were found in many fields, but dense reproduction was limited to a few fields. Habitat data were gathered from these fields to learn something of the range of sites on which sweetgum can become established in fairly high numbers.

To localize observations in each of these fields, a 4 x 4 m quadrat was placed at the approximate farthest distance from the seed source where it was still possible to have at least 10 seedlings per quadrat (about 2500/acre). (In some cases it was impossible to reach this distance, due to limitations of the field, disturbance, etc.) In this way, a rough estimate was obtained of the effective seeding range of sweetgum seed. This information will be used later in the general discussion.

The soil under each quadrat was identified and a sample was taken from both the A and the B horizons for textural analysis. Each site in the immediate vicinity of the quadrat was classified as either dry, intermediate, or moist. This was done on the bases of the underlying soil, the topography, and the type of herbaceous vegetation occurring there. Exceptionally wet sites were not considered in this survey.

The results obtained from these observations are given in Table 1. It is apparent from these data that when there is adequate seeding and favorable weather conditions, sweetgum is able to invade, "en masse," a wide range of upland old-field sites. It was found on a variety of topographic positions, on dry and moist sites, and on soils varying from Mayodan, a light friable soil, to Whitestore (red phase), one of the heaviest and most plastic of Piedmont soils.

In passing, it may be noted (Table 1) that, in all but one instance, dense sweetgum reproduction was associated with coarse textured A horizons. Coile (1950), studying the density of hardwood reproduction under pine stands, noted a similar relationship. He found that sweetgum attained greater densities on coarse textured A horizons than it attained on fine textured ones.

Although sweetgum is capable of mass invasions of many types of sites, its best reproduction seemed to be associated with the more moist sites. Most of the fields represented in Table 1 were judged to be intermediate or moist. Field number 11 represented the only "dry" site where good reproduction was found.

Apparently the establishment of sweetgum is more dependent on moisture than is the establishment of pine. This was shown, particularly, by certain fields where pine reproduction was common throughout the field, while dense sweetgum reproduction was limited to ditch banks or moist spots within the field. In these fields it appeared that seed source could not have been the controlling factor, but that the establishment of both species was related to their specific tolerances to moisture conditions.

In general, it seems from these observations that sweetgum establishment in upland abandoned fields is more restricted by environmental conditions than is the establishment of loblolly pine. To determine more exactly the causes for this difference in tolerance to old field conditions, studies in relative germination and relative survival were undertaken. Particular stress was placed on the role of soil moisture.

SECTION III. THE EFFECTS OF DRYING ON GERMINATING SEEDS OF BOTH SPECIES

The successful invasion of old-fields by either sweetgum or pine is dependent, first, on successful germination of the seed. Experiments with white pine (Smith 1951) showed losses after germination exceeding those at germination in only one case.

The importance of the effect of drying during germination was indicated in an experiment on the drought endurance of seedlings when a number of

Table 1. Habitat data on old-field sites supporting dense sweetgum reproduction.

Area	Density of seedlings/ quadrat	Number feet from seed source	Soil Series	Texture of A horizon	Texture of B horizon and estimated friability	Topography	Estimated moisture regime
1.......	50	97	Mayodan	Sandy loam	Friable sandy clay loam	Flat	Intermediate
2.......	49	118	Mayodan	Sandy loam	Semi-friable clay loam	Flat	Intermediate
3.......	15	124	Bucks	Sandy loam	Plastic clay	Flat	Moist
4.......	50	92	Durham	Sandy loam	Semi-friable clay loam	Gentle slope	Intermediate
5.......	29	150	Appling	Sandy loam	Semi-friable clay loam	Gentle slope	Intermediate
6.......	17	80	Cecil	Sandy loam	Semi-friable sandy clay loam	Gentle slope	Intermediate
7.......	14	205	Colfax	Loamy sand	Semi-friable sandy clay loam	Gentle slope	Moist
8.......	22	147	Whitestore (red phase)	Sandy loam	Plastic clay	Flat	Moist
9.......	11	197	Creedmore	Sandy loam	Semi-plastic clay loam	Gentle slope	Moist
10.......	18	100	Penn	Sandy clay loam	Semi-plastic clay	Gentle slope	Intermediate
11.......	11	147	Granville	Loamy sand	Semi-friable sandy clay loam	Ridge top	Dry
12.......	50	70	Creedmore	Sandy loam	Plastic clay	Flat	Intermediate

TABLE 2. The Effect of Drying On Germinating Seeds of Loblolly Pine and Sweetgum.

Days of drying	Number of Seeds in Soil		Germination Measured From The Start of Drought			
	Pine	Sweetgum	20 days		51 days	
			Pine	Sweetgum	Pine	Sweetgum
0......	27	15	17	1	22	1
2......	16	9	7	0	7	0
4......	19	17	4	0	4	0
8......	28	16	0	0	8	0
16......	21	10	0	0	2	0

ungerminated seeds of sweetgum and loblolly pine were subjected to various periods of drought. Following rewatering, the pine seed continued to germinate while the sweetgum seed did not (Table 2).

Evidently there was a marked difference in the ability of these seeds to resume germination after drying. This apparent difference would favor the establishment of pine on the upland old-fields, particularly those with little cover or mulch; for as Smith (1951) and Russel (1939) have shown, such areas are subject to rapid fluctuations of surface moisture.

A germination experiment was designed to test, more precisely, the relative effects of drying on germinating seeds of loblolly pine and sweetgum.

METHOD

Two germinators of the design of Toumey & Stevens (1928) were used. Each was composed of eleven 6-inch funnels inverted over filter paper which was supported 1 in. above a water surface maintained at a constant level and kept moist by cheesecloth wicks. This kept the seeds moist, yet adequate aeration was afforded by the openings in the funnels.

Three groups of about 40 seeds of each species were placed under each funnel. When about 15% of the seeds of a species had germinated, they were discarded and those remaining were subjected to three treatments: (1) no drought, (2) 48-hour drought, (3) 120-hour drought. Group (1) was left in the germinator continuously. Drought was simulated for the other two groups by placing them in a desiccator (relative humidity 45-55%; 21°C) for the required time. After treatment the seeds were returned to their respective germinators. All final counts are based on 47 days of hydration in the germinators, including several days prior to treatment.

The seeds used were collected locally in the autumn of 1950, and stored dry at 5°C until June, 1951. Weak seeds (light weight) were then removed by flotation and the remainder stratified in moist vermiculite (5°C) for 20 days. On July 25, 1951, the seeds were randomly grouped, soaked in 2% sodium hypochlorite for 10 minutes and placed in the germinators without washing.

The data for sweetgum were statistically analyzed by regression analyses, while pine comparisons were based on the variance of weighted means.

RESULTS AND DISCUSSION

Following drying, the tips of the radicles of many germinating sweetgum seeds were discolored (brown). Marking with India ink revealed that they were not actively growing (elongating). Evidently they had been injured while still within the seedcoat and their seeming emergence had resulted when the elongating hypocotyls had pushed the seedcoats away from them. Occurrence of this phenomenon under field conditions would mean that the radicle would remain exposed to the air and out of contact with the mineral soil. The longer this situation existed the less would be the chances for seedling establishment (Pomeroy 1948).

In most cases the radicles with brown tips either died completely, or after several days resumed growth in the form of small side roots behind the injured tip. Some, however, did resume tip growth after a day or two. These were counted as normally germinated. All others, since their chances of establishment were lessened because of browning, were counted as abnormally germinated.

The results are presented in Figs. 4 & 5 and in Table 3.

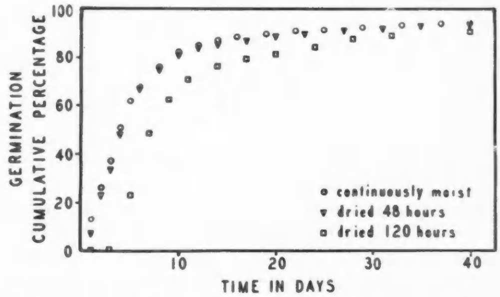

FIG. 4. The effect of drying on germinating loblolly pine seed.

TABLE 3. The Effect of Various Lengths of Drying On Germinating Seed of Sweetgum and Loblolly Pine. All counts are based on 47 days of germination excluding the drying periods.

Species	Drying period (hours)	Disposition of Seed After 47 Days				
		Browned radicles	Dead	Viable, but ungerminated	Germinated	Tota
Sweetgum	0	1	30	56	577	664
	48	70	29	173	382	654
	120	86	33	208	338	665
Pine	0	1	18	25	706	750
	48	1	13	31	707	752
	120	6	35	28	667	736

From Table 3 and Fig. 4 it is apparent that the rate and amount of pine germination was hardly affected by the drying treatment. Statistically the difference between total germinations in the 0-hour and 48-hour treatments was not significant. More-

over the difference between both of these treatments and the 120-hour treatment was significant only at the 5% level. Rohmeder & Kaiser (1951) obtained similar results with *Pinus sylvestris* and *Picea excelsa*.

The rate and amount of sweetgum germination was severely reduced by both drying treatments (Table 3, Fig. 5). The 48-hour treatment was almost as damaging as the 120-hour treatment, since the difference between them was significant only at the 5% level. This represents a small degree of significance considering that the 120-hour treatment was two and one-half times longer than the 48-hour treatment.

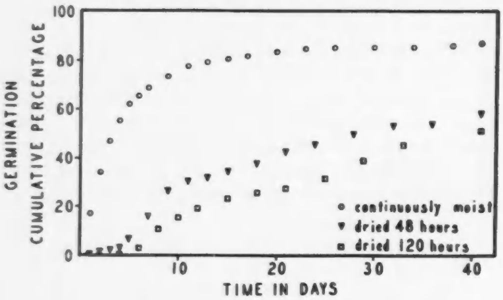

FIG. 5. The effect of drying on germinating sweetgum seed.

Evidently, the greatest amount of damage occurred somewhere between the 0-hour and the 48-hour treatment.

There was no significant difference between the 48-hour and 120-hour treatments in pre-emergence injury to sweetgum radicles. Apparently a certain proportion of the germinating seeds were susceptible to injury of this type, and between 0 and 48 hours of drying was sufficient to cause maximum damage.

Browning or pre-emergence injury to radicles (root primordia) reduced successful sweetgum germination by about 12%, but did not at all affect the germination of pine. Perhaps pine was more resistant to this type of injury because of inherent physiological resistance or because its thick seedcoat prevented rapid drying. The latter explanation seems more likely since, following germination, the resistance of radicles of both species to drying was poor. Drying at room temperature for three hours severely injured the root tips of 55 out of 56 sweetgum and 27 out of 37 pine. Even under these conditions, however, pine roots appeared to be more resistant to drying than those of sweetgum.

Drying treatments hardly increased the numbers of pine seeds that remained viable but ungerminated, while the numbers of sweetgum seeds in this category were greatly increased. It is likely that most seeds in this condition would not have germinated even if the germination period had been extended, because the rate of germination at the end of the period was low and still declining.

In the field, seeds whose germination had been delayed probably would not produce seedlings for the following reasons: (1) Many would be unable to germinate, regardless of environmental conditions, for a month or so following drying. (2) Delayed germination might result in seedlings too young to endure summer heat or drought. (3) Some seeds could not germinate at all. (4) They would be more susceptible to attack by fungi.

It is apparent that slight drying during germination caused a large reduction in the successful germination of sweetgum seeds. Pine seeds, however, were hardly affected. In the old-fields, this difference could be of major importance since it would tend to favor pine over sweetgum, particularly on sites subject to frequent surface drying during the spring.

SECTION IV. THE RELATIVE SURVIVAL OF SWEETGUM AND LOBLOLLY PINE SEEDLINGS

Very little is known about the factors controlling the survival of loblolly pine seedlings under old-field conditions. Chapman (1942) and McQuilkin (1940) noted that pine mortality is apt to be high during the first season following germination and that soil moisture is an important controlling factor. Barrett (1940) pointed out that in Buckingham County, Virginia, 85% of the loblolly seedlings that germinated in the spring of 1939 survived through October, while 50% of those germinating in Union County, South Carolina, died before early summer. He thought that the difference in survival was due to differences in rainfall. Buckingham County had better than average rainfall, while Union County was characterized by sub-normal rainfall and drought.

Even less is known about the factors controlling the survival of sweetgum seedlings. It is believed, however, that their survival is dependent to a large degree on relatively high soil moisture prior to the development of a tap root (Trenk 1929).

Apparently the survival of both species is closely related to soil moisture conditions. Pine, however, does not appear to be as sensitive to low soil moisture as does sweetgum. This was indicated by the field observations discussed in Section II. Experiments were conducted to ascertain, in part, the relative survival of each species. Particular emphasis was placed on determining the degree to which each was dependent on soil moisture. They were as follows: (1) The relative drought endurance of seedlings under 1 year of age. (2) Relative survival during the first growing season under various old-field conditions. (3) The relative drought endurance of 2-year-old seedlings.

THE RELATIVE DROUGHT ENDURANCE OF SEEDLINGS UNDER ONE YEAR OF AGE

Four clusters of 5 sweetgum and 5 loblolly pine seed were planted in Durham loamy sand in each of 70 clay bulb pots (#9) and rye grass seed was sown between the clusters. The pots, following germination, were kept in the greenhouse in full sunlight until July, when because of excessively high temperatures they were moved to a shady room.

At four different times during the growing season

a group of pots was selected from the original number and subjected to drought. First, the tree seedlings in each pot were thinned to 4 of each species and 3 sunflower seeds were planted in each pot. When the sunflowers had grown to a reasonable size, watering was discontinued and a 1-in. layer of vermiculite was spread over the soil and around the stems of the seedlings to reduce surface evaporation and extremes of soil temperature. The pots, framed with cardboard and with glasswool tightly packed around them, were kept in full sunlight.

The rye grass with its extensive root system rapidly and uniformly reduced soil moisture. When the more sensitive sunflowers remained wilted overnight, the soil mass was assumed to be at the wilting percentage. Determinations made at several levels in several pots indicated that this was so.

At this time the pots were removed to a shaded room and the periods of drought treatment began. At the end of the respective drought periods, watering was resumed and after one day the pots were returned to the bench in full sunlight. Survival counts were made 7 to 14 days later.

The age levels of the seedlings (measured from the time of seed planting) and the various drought periods (the length of time that the soil was at or below the wilting percentage) to which they were subjected are presented in Table 4.

TABLE 4. Schedule of Drought Treatments.

Group	Age of seedlings in days	Sub-groups and Number of Hours of Drought to Which Each Was Subject.						
		1	2	3	4	5	6	7
1......	39	0	48	96	192	384		
2......	71	0	48	96	192	384		
3......	119	0	48	96	144	192		
4......	163	0	24	48	72	96	120	144

The sub-groups of pine and sweetgum were each composed of 11 or 12 seedlings distributed in 3 pots. A few pots contained only 3 seedlings of a species, while all of the pots in the 144-hour treatment of the 163-day age level contained only 5 sweetgum seedlings.

RESULTS AND DISCUSSION

It appears from the data that seedlings of loblolly pine, at all ages tested, were better able to endure drought than were seedlings of sweetgum (Table 5). In every period of drought where any survival was recorded, the pine exceeded the sweetgum by 15% to 50%. At the 39- and the 163-day age levels some pine survived 48 hours more than did the longest-surviving sweetgum.

Some question might be raised as to whether direct temperature injury (of the type described by Hartley 1918; Baker 1929; etc.) had caused some mortality prior to wilting. Probably this type of injury was negligible since those seedlings that were rewatered

TABLE 5. The percentage survival of loblolly pine and sweetgum seedlings of various ages under various periods of drought.

Drought (hours)	Age of Seedlings in Days							
	39		71		119		163	
	Pine	Gum	Pine	Gum	Pine	Gum	Pine	Gum
0.......	92	100	100	100	100	100	100	100
24.......	..	..	..	..	..	..	100	100
48.......	83	42	100	100	100	58	100	58
72.......	..	..	..	..	..	..	100	73
96.......	25	0	67	17	0	0	42	25
120.......	..	..	..	..	..	..	25	0
144.......	..	..	..	..	0	0	13	0
192.......	0	0	0	0	0	0		
384.......	0	0	0	0				

as soon as the soil moisture reached the wilting percentage showed a mortality of only 1 out of 96. Apparently, most of the mortality was the result of drought or drought-temperature interaction following the reduction of the soil moisture to the wilting percentage.

Since soil moisture had been uniformly reduced to the wilting percentage, root extension could not have been a factor in the differential drought endurance of the two species. Rather, it probably resulted from inherent differences in the drought resistance of the two species.

Because the resistance of seedlings to adverse conditions is generally thought to increase with age, it is appropriate to emphasize that the 119- and the 163-day-old seedlings, of both species, failed to exhibit any greater endurance than the 71-day-old seedlings. In fact, the survival of the 119-day-old seedlings was below that of the 71-day-old seedlings.

This difference in survival between age groups was probably related to differences in temperature during the testing periods. To indicate the various temperature regimes, maximum temperatures were averaged for the first four days of each period (Durham Weather Station data). The averages were as follows: 39-day run, 19°C; 71-day run, 27°C; 119-day run, 34.5°C; and 163-day run, 30°C. During the 119-day run, the period of highest outdoor maximum temperatures, a maximum temperature of 49°C was recorded in the greenhouse.

Apparently increased temperature (higher maximum temperatures, or longer duration of high temperatures) made the drought more effective in causing higher seedling mortality. Bates & Roeser (1924), working with Rocky Mountain species, also concluded that extreme heat must often kill seedlings which would be able to tolerate existing drought conditions.

Loblolly pine, regardless of temperature, maintained about the same favorable margin of survival over sweetgum. Evidently it has inherently greater endurance to drought conditions, not only at all of the ages tested, but also under conditions of high or moderate temperatures.

Relative Survival during the First Growing Season Under Various Old-field Conditions

METHOD

On April 14, 1951, previously stratified seeds of both species were sown in 36 plots located on 9 different and widely separated upland broomsedge fields especially chosen to represent a wide range of Piedmont soil conditions. All fields were topographically similar, flat or slightly undulating, with fair to good surface drainage.

Soil samples from each field were analyzed for texture, moisture equivalent, and wilting percentage of both the A and B horizons. Fields with similar B horizons were grouped as having (1) heavy subsoils, (2) medium subsoils, (3) light subsoils (Table 6).

TABLE 6. Analysis of Soils.

Field	A Horizon			B Horizon		
	Wilting percent	Moisture equiv.	% 2 *mu* clay	Wilting percent	Moisture equiv.	% 2 *mu* clay
			LIGHT SUB-SOILS			
1......	1.6	4.4	4.7	1.6	6.6	7.8
8......	2.5	6.7	6.0	5.1	12.7	14.5
2......	1.6	5.0	6.7	6.7	15.6	25.4
			MEDIUM SUB-SOILS			
10......	2.3	6.2	6.7	14.7	20.9	33.2
4......	2.7	9.1	7.3	15.7	26.3	36.4
3......	4.3	11.4	13.5	13.9	24.4	37.5
			HEAVY SUB-SOILS			
7......	6.3	14.0	11.1	27.8	44.1	56.7
5......	3.8	11.7	8.2	23.0	36.0	58.3
9......	4.5	10.3	9.3	22.5	50.2	59.7

Four plots, 3 ft. square, were randomly located on each field. Two plots were spaded, and on two the broomsedge was left undisturbed. It was hoped that this procedure would give information on the capacity of each species to survive under conditions frequently met in old-fields (namely, recently abandoned fields with areas of bare soil, and fields on which succession has proceeded to the broomsedge stage).

The first seedling count was made on May 26 and thereafter three survival counts were made at various times. The data for each species from each count were subjected to regression analysis using the following equation:

$$\text{Probit of survival} = b_o + b_1X_1 + b_2X_2 + b_nX_n$$

It was solved by the method of least squares and an analysis of variance was calculated. From the analysis of variance, tests (F-variance ratio) of significance were made of the independent variables. Numerical coefficients were calculated for the significant variables and substituted in the equation. The equation was then used to calculate the adjusted means with the effect of the insignificant variables eliminated.

Five independent variables were used for the data from the June 8 survival count (see Table 8 for the variables used). Three independent variables were used in the analyses of all data collected after June 8 (see Table 9 for the variables used). This was necessary because the basis for the extra two variables was lost when the 12 plots in fields 1, 3, and 4 were destroyed by plowing. Thereafter the plots on fields 2, 8, and 10 were considered as belonging to one soil group and called the light-medium soil group.

SURVIVAL FROM MAY 26 TO JUNE 8

The first survival count was made on June 8 immediately following the final phase of a prolonged spring drought. Between May 7 and May 23 the Durham Weather Station recorded only three light rains totalling 0.74 in., while from May 24 to June 5 no rainfall was recorded. The drought was broken by 0.36 in. of rainfall on June 5 and 6, and the seedlings were recounted on June 8. It was hoped that the losses during this period, May 26 to June 8, would represent the reaction of each species to prolonged moisture stress under field conditions.

RESULTS AND DISCUSSION

The total survival counts for both species are given in Table 7, while results of the F-variance ratio tests from the analyses of variance of these data are

TABLE 7. Survival of Seedlings Less Than One Year of Age Growing Under Various Old-Field Conditions, May Through October, 1951.

Soil Group	Loblolly				Sweetgum			
	Broomsedge		Spaded		Broomsedge		Spaded	
	MAY 26 THROUGH JUNE 8							
	May	June	May	June	May	June	May	June
Light..............	69	12	147	90	120	7	262	85
Medium...........	101	82	111	79	202	70	153	67
Heavy.............	136	121	109	100	179	135	208	131
Total...........	306	215	367	269	501	212	623	283
	JUNE 8 THROUGH AUGUST 25[1]							
	June	Aug.	June	Aug.	June	Aug.	June	Aug.
Light-medium......	10*	6	98	64	44*	25	133	30
Heavy.............	144*	123	107*	87	144*	128	131	35
Total...........	154	129	205	151	188	153	264	65
	AUGUST 25 THROUGH OCTOBER 17							
	Aug.	Oct.	Aug.	Oct.	Aug.	Oct.	Aug.	Oct.
Light-medium......	7*	7	44[2]	25	25	22	29[2]	25
Heavy.............	123	122	87	84	128	109	35	32
Total...........	130	129	131	109	153	131	64	57
	MAY 26 THROUGH OCTOBER 17[3]							
	May	Oct.	May	Oct.	May	Oct.	May	Oct.
Light-medium......	23	7	95	25	117	22	236	25
Heavy.............	149	122	116	84	188	109	208	32
Total...........	172	129	211	109	305	131	444	57

[1]Twelve plots destroyed during July.
[2]One plot destroyed during September.
[3]Does not include plots destroyed during period.
*Number includes new germinations.

TABLE 8. Results of the F-variance ratio tests from the analyses of variance based on the survival data from May 26 to June 8.

Variable	Description of variable	Pine	Sweetgum
X1	Difference in survival between heavy and light soils	Significant (1% level)	Significant (1% level)
X2	Difference in survival between ½ (heavy +light soils) and medium soils	Not significant	Not significant
X3	Difference in survival between broomsedge and spaded areas	Not significant	Not significant
X4	Interaction between X1 and X3	Not significant	Not significant
X5	Interaction between X2 and X3	Not significant	Not significant

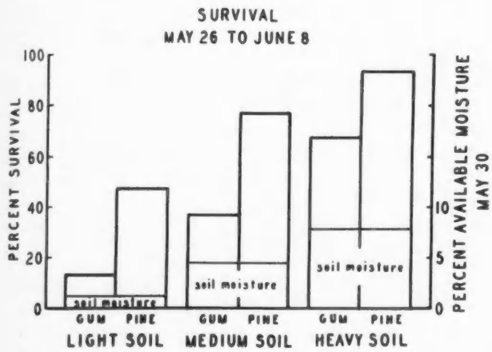

FIG. 6. Adjusted means of survival for sweetgum and loblolly pine.

given in Table 8. The adjusted means of survival for each species are presented in Fig. 6.

The difference in survival of both species on heavy and light soils was highly significant (Table 8). The X_2 variable, a test for non-linearity of survival, was not significant for either species. In other words, the survival of each species was linear over the three soil groups, being least on light soils, intermediate on medium soils, and most on heavy soils.

To gain some idea of the degree that soil moisture stress limited survival, 4 soil samples (2 from broomsedge and 2 from spaded areas) were collected from each field on May 30. The samples were taken from the A horizons at a depth of 5 in. This proved to be 2 in. lower than the maximum root penetration of either species as shown by excavation of several seedlings on June 8. The percentage of available water in each sample was determined in the laboratory. The adjusted means of soil moisture for each group are presented in Fig. 6.

No consistent differences in available water were found between broomsedge and spaded areas on the same soil. A similar lack of consistent soil moisture differences at this depth between grass and denuded plots have been reported by Pessin (1938).

There were distinct differences in soil moisture between soil groups, with light soils having the least and with heavy soils having the most. Apparently these differences were associated with the water holding capacity of the A horizon and the permeability of the B horizon. Since the measurements were made on May 30, they represent conditions 5 days before the end of the drought. Therefore, it may be assumed that even more rigorous conditions existed at the height of the drought 5 days later.

Figure 6 shows the inter-relationship between soil moisture, soil group, and the survival of both species. Apparently the difference in survival on the various soil groups was due to differences in soil moisture between them. However, the difference in survival between species on any one soil group was probably related to an inherent difference in tolerance to moisture stress or moisture stress-temperature interaction. The existence of such a difference already has been indicated by results previously described.

Root penetration might have been a factor in the differential survival of sweetgum and pine. Toumey & Neethling (1923, 1924) have shown how variability in initial root habits can account for differences in survival during dry periods. The initial roots of some species are able to penetrate the soil quickly and deeply following germination. Consequently, soon after germination they are affected but little by moderate drought which desiccates the soil from the surface downward. The roots of other species, with slower rates of penetration, may not have grown beyond the zone of extreme moisture stress and therefore succumb to the drought.

In the present instance, although root penetration might have been a factor in survival, excavated seedlings of both species had roots that seemed to be of nearly the same magnitude and distribution. However, this point needs closer investigation under controlled conditions.

There was also a possibility that injury due to high temperatures of the surface soil might have contributed to the reduction in survival. This effect, however, was probably at a minimum since there was no significant difference in broomsedge-shaded or unshaded-spaded areas (Table 8). It is likely that this would not have been the case if pre-drought injury due to excessive surface temperatures had been important. For as Hartley (1918), Korstian & Fetherhof (1921), Pessin (1938), and Smith (1951) have pointed out, the least bit of shade is generally effective in markedly reducing the injury due to high surface temperatures.

SURVIVAL FROM JUNE 8 TO AUGUST 25

The second survival count was made on August 25. It was hoped that this count would give some indication of relative survival of the two species during the hot summer months.

During this period the average maximum temperatures recorded by the Durham Weather Station were as follows: June 8 to 30, 30°C; July 1 to 31, 33.5°C; August 1 to 25, 33°C. The total precipitation was 4.02 in. from June 8 to 30, 0.22 in. from July 1 to 19,

2.96 in. from July 20 to 31, and 2.49 in. from August 1 to 25. The rainfall was considerably below the 17-year average with deficits of 1.24 in. and 2.21 in. in July and August, respectively.

RESULTS AND DISCUSSION

The total survival counts for both species are given in Table 7, while the results of the F-variance ratio tests based on the analyses of these data are given in Table 9. The adjusted means of survival are presented in Fig. 7.

TABLE 9. Results of the F-variance ratio tests from the analyses of variance based on the survival data from June 8 to August 25.

Variable	Description of variable	Pine	Sweetgum
X1	Difference in survival between heavy and light-medium soils	Significant (5% level)	Significant (1% level)
X2	Difference in survival between broomsedge and spaded areas	Not significant	Significant (1% level)
X3	Interaction between X1 and X2	Not significant	Not significant

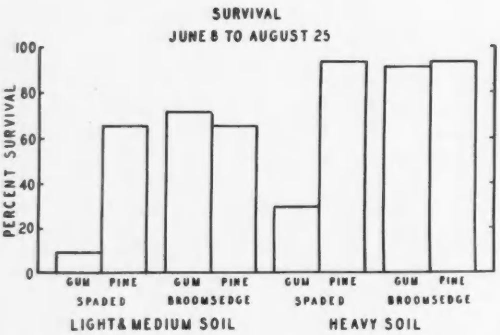

FIG. 7. Adjusted means of survival for sweetgum and loblolly pine.

For both species, survival is significantly better on heavy soils (Table 9). For pine, the difference in survival between broomsedge and spaded areas is not significant, but for sweetgum this difference is highly significant.

In broomsedge the survival of both species is about equal, but in spaded areas pine survival is far greater than that of sweetgum (Fig. 7). On spaded-light-medium soils it is about 6 times greater, while on heavy soils it is approximately 3 times greater.

The cause of this difference in survival between species on sparsely vegetated or spaded areas is not known, but it might be associated with a differential species response to light and temperature conditions (isolated temperature measurements made one-eighth inch below the soil surface showed spaded areas to be as much as 15.5°C warmer than corresponding broomsedge areas). Whatever the cause, the inability of sweetgum seedlings to endure conditions on spaded or open areas could be of major importance in limiting its establishment in recently abandoned fields.

SURVIVAL FROM AUGUST 25 TO OCTOBER 17

The third and final count was made on October 17. Its purpose was to give information on survival for the time between the hot summer months and the first frost.

The average maximum temperatures for this period were 30.5°C for the last 6 days in August, 29°C for September, and 27°C for the first 17 days in October (Durham Weather Station Data). Rainfall was abnormally low. The total for September was 1.29 in., 1.79 in. below the 17-year average. From September 16 to October 8 only 0.12 in. of rainfall was recorded.

RESULTS AND DISCUSSION

The total survival counts for both species are given in Table 7, and the results of the F-variance ratio tests based on the analyses of variance of these data are given in Table 10. The adjusted means of survival are presented in Fig. 8.

There were no significant differences in the survival of sweetgum on heavy and light-medium soils or on spaded and broomsedge areas. The difference in pine survival between spaded and broomsedge

TABLE 10. Results of the F-variance ratio tests from the analyses of variance based on the survival data from August 25 to October 17.

Variable	Description of variable	Pine	Sweetgum
X1	Difference in survival between heavy and light-medium soils	Significant (1% level)	Not significant
X2	Difference in survival between broomsedge and spaded areas	Not significant	Not significant
X3	Interaction between X1 and X2	Not significant	Not significant

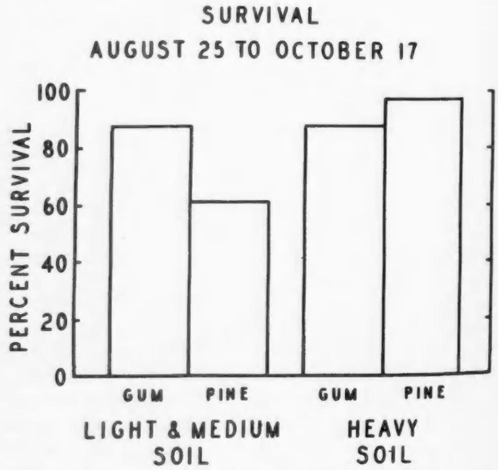

FIG. 8. Adjusted means of survival for sweetgum and loblolly pine.

areas was insignificant, but between heavy and light-medium soils it was highly significant (Table 10).

In general, the survival of both species on heavy soils was about equal, although on light-medium soils the survival of sweetgum was about one and one-half times greater than that of pine (Fig. 8).

The percentage of pine survival during this period showed little change from that of the summer period on comparable areas. The rate of sweetgum survival increased greatly in spaded areas on both soil groups and slightly in broomsedge on light-medium soils.

The increase in sweetgum survival might have been associated with the progressive development of its tap root. At any rate, it occurred with the advent of generally lower temperatures and in spite of very subnormal rainfall during September. It might be that this increase is the first indication of the higher tolerance to old-field conditions exhibited by older sweetgum seedlings.

TOTAL SURVIVAL FROM MAY 26 TO OCTOBER 17

Total survival of both species was based on the starting number of seedlings on May 26, plus any that germinated during the season, and the number of seedlings surviving on October 17. Counts from plots destroyed during the growing season are not included in the starting number.

RESULTS AND DISCUSSION

The total survival counts for both species are given in Table 7, while results of the F-variance ratio tests based on the analyses of variance of these data are given in Table 11. The adjusted means of survival are presented in Fig. 9.

TABLE 11. Results of the F-variance ratio tests from the analyses of variance based on the survival data from May 26 to October 17.

Variable	Description of variable	Pine	Sweetgum
X1	Difference in survival between heavy and light-medium soils	Significant (1% level)	Significant (1% level)
X2	Difference in survival between broomsedge and spaded areas	Not significant	Significant (5% level)
X3	Interaction between X1 and X2	Not significant	Not significant

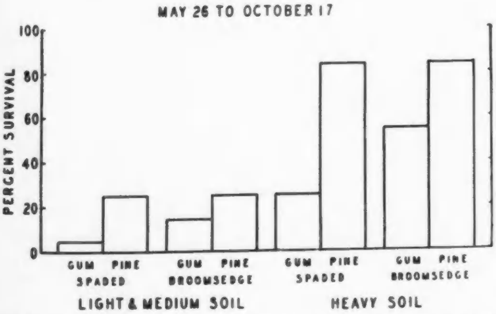

FIG. 9. Adjusted means of survival for sweetgum and loblolly pine.

The survival of both species on heavy soils is significantly greater than on light-medium soils (Table 11). The difference in pine survival on broomsedge and spaded areas is not significant, indicating that the survival of pine was independent of the broomsedge stage in succession (Coile 1940, and McQuilken 1940, reached the same conclusion following extensive field observations). Contrariwise, the differences in the survival of sweetgum on broomsedge and spaded areas are highly significant, indicating that its survival was greatly increased by the presence of the broomsedge. This difference can be traced to the inability of sweetgum seedlings to tolerate conditions on bare or sparsely vegetated areas during the hot summer months.

Pine survival exceeded that of sweetgum on all areas, particularly on spaded areas where its survival was about six times greater on light-medium soils and about three times greater on heavy soils (Fig. 9). This suggests that pine would be more successful than sweetgum in invading old-fields, particularly recently abandoned fields prior to the development of broomsedge or other dense vegetation.

The superior tolerance of pine (seed and/or seedlings) to bare soil conditions was clearly shown on one upland old-field, half of which was in broomsedge and half of which had been used as a garden the previous year. Both halves were located near seed sources of both species. Pine reproduction was found on both halves, but sweetgum was almost entirely limited to the broomsedge half.

From the foregoing it is apparent that pine, during some years, could become established in quantity a year or more before similar establishment by sweetgum (under the same conditions of seeding). This could be a decided advantage to the pine, not only because it would gain time, but also because its earliest growth would be unhindered by broomsedge competition.

The superior ability of pine to survive under all old-field conditions probably contributes to its general ascendancy over sweetgum in abandoned upland fields. However, superior survival alone is not the single controlling factor. If survival alone were the controlling factor, it is probable that sweetgum would be more prominent in old-fields than it is.

THE RELATIVE DROUGHT ENDURANCE OF TWO-YEAR-OLD SEEDLINGS

METHOD

Eighteen 2-year-old potted seedlings of each species were used in this experiment. Prior to treatment, each seedling had grown in greenhouse loam, out of doors, for at least 7 months.

The plants were randomly divided into 3 groups of 12, including 6 of each species. Beginning on July 23, 1951, each group was subjected to one of the following treatments: (a) soil at or below the wilting percentage for 4 days, (b) for 6 days, and (c) for 8 days. Treatment began when sunflowers growing in each pot remained wilted overnight. Follow-

ing treatment, the plants were watered daily and closely observed for a period of one month.

The experiment was conducted in the greenhouse under conditions of full light. Throughout, the temperature was recorded by a Bachrach Tempscribe.

RESULTS AND DISCUSSION

All of the seedlings of both species in the 6- and 8-day treatments died. Four sweetgum and no pine seedlings survived the 4-day treatment. This low rate of survival was probably related to the extremely high greenhouse temperatures during the treatment periods. On most days, the temperature remained above 38°C for at least 5 hrs. The average daily maximum temperature for the whole period was 45.5°C.

Unfortunately, since all of the pine seedlings died, no real measure of relative drought endurance was obtained. However, the results suggest that the drought endurance of 2-year-old sweetgum seedlings is at least equal to that of 2-year-old pine. This is in agreement with the findings of Wenger (1952). Since, at younger ages, pine appeared to have greater drought endurance (Table 5), it seems that the endurance of sweetgum increased disproportionally with age.

From field observations, it was apparent that the survival of both species increased with age. This was shown during the May, 1951, drought. Many seedlings of both species originating in 1951 and some of those starting in 1950 died, while those dating from 1949 or thereabout were practically unaffected. During the remainder of the growing season all seedlings, except those originating in 1951, showed little mortality.

The increase in sweetgum survival was associated with the development of a tap root (sweetgum develops a deep tap root in upland situations, Chittenden 1906). Trenk (1929) has reported that once the tap root begins to develop, the tree will grow persistently on gravelly hillsides or on heavy clay.

It is evident that the survival of seedlings of both species increases with age. Probably, once the roots of either species become established in the relatively root-free subsurface soil of abandoned fields, survival is no longer a problem until the forest stand closes and competition for light and water begins.

In some areas the differential response of the two species to fire would also have to be considered. Oosting (1944) found that 35-year-old overstory pine was practically unaffected by surface fire. Similarly, Ashe (1915) and Chapman (1942) noted that the fire resistance of pine was relatively great after the first few years of growth. To the contrary, the fire resistance of sweetgum was found to be very poor (Trenk 1929, Chapman, 1942). Consequently, surface fires in young mixed stands could eliminate sweetgum from the overstory and thus change the composition of the first arboreal stage in old-field succession.

Severe crown fire in a pure pine stand can result in the development of a mixed pine-hardwood stand. Following a destructive crown fire in a 35-year-old pine stand, Oosting (1944) noted that pine seedlings became established so rapidly that they were able to compete successfully with surviving hardwood saplings and sucker sprouts resulting from the fire. This area at present, 21 years after the fire, supports a mixed pine-hardwood stand.

SECTION V. HEIGHT GROWTH AS A FACTOR IN OLD-FIELD SUCCESSION

During 1950 and 1951 numerous observations were made of the first forest stands to develop on abandoned fields in a search for evidence that differential height growth is of importance in determining which species becomes the first arboreal dominant in old-field succession.

The preliminary observations indicated that old-field stands are of three general types: (1) the great majority have an overstory of pure pine. Although there is no sweetgum in the overstory, there is commonly a heavy understory of uneven-aged sweetgum. (2) The second type, apparently rare, has an almost pure pine overstory with occasional, or rarely several, sweetgum trees as codominants. Some mixed stands of this type may have been overlooked because they were mistaken for mixed stands developed on cut-over or burned-over areas. (3) The third and very rare type is the pure stand of upland sweetgum.

To determine whether some of the understory sweetgum was of the same age as the overstory pine in the stand, or whether overstory sweetgum was older than overstory pine in the same stand, age, height, and d.b.h. measurements were made. In 8 stands (types 1 and 2), one large understory sweetgum tree and the largest overstory pine growing within 20 ft. of that sweetgum were measured. In 13 type 2 stands, one overstory sweetgum and the largest overstory pine growing within 20 ft. of it were also measured. Height was determined by the use of a clinometer, age was based on the average of two increment borings, and d.b.h. was measured with a diameter tape.

The data presented in Table 12 show that overstory pine was definitely older than understory sweetgum. In all but one instance (stand 13) it appeared that the difference in height was attributable to a difference in age. This minimized the possibility that the pine gained dominance over sweetgum of the same age because of more rapid height growth. Apparently the sweetgum seeded in after the pine, made fairly rapid height growth, and soon formed an advanced understory.

It was noted, from these and subsequent measurements, that sweetgum invasion often occurred 5 to 10 years after the establishment of pine. Evidently good conditions prevailed at that time for the germination and establishment of sweetgum. Since it has already been shown that sweetgum can become established on abandoned fields, it is puzzling that no reproduction of the same age as the pine could be found. This suggests that no sweetgum seed reached

TABLE 12. A comparison of height and diameter growth of sweetgum and pine growing together in upland old-field stands.

Stand Number	Pine			Sweetgum			Difference (P - S)		
	Age	Height feet	d.b.h. inches	Age	Height feet	d.b.h. inches	Age	Height feet	d.b.h. inches
Overstory Pine and Understory Sweetgum Trees From Type 1 and 2 Stands									
16	17	37	7.8	11	23	2.2	6	14	5.6
3	18	25	4.5	14	18	1.8	4	7	2.7
13	21	51	9.5	16	19	2.8	5	32	6.7
18	21	30	6.7	14	25	2.8	7	5	3.9
4	22	30	5.8	13	23	3.4	9	7	3.4
14	27	42	11.2	16	23	3.3	11	19	7.9
2	32	50	10.5	23	38	5.5	9	12	5.0
1	75	65	15.0	59	40	7.4	16	25	7.6
Overstory Trees From Type 2 Stands									
10	9	19	3.8	9	19	2.3	0	0	1.5
7	11	22	4.0	9	18	2.0	2	4	2.0
9	14	26	5.0	17	29	4.4	−3	−3	0.6
6	15	24	5.5	14	20	3.0	1	4	2.5
11	15	32	5.8	15	33	5.1	0	−1	0.7
15	15	31	4.8	14	27	3.4	1	4	1.4
8	16	40	10.3	16	39	5.7	0	1	4.6
13	21	51	9.5	22	53	7.8	−1	−2	1.7
5	22	42	7.5	22	41	5.9	0	1	1.6
17	26	38	15.0	24	34	6.1	2	4	8.9
14	27	42	11.2	31	44	10.0	−4	−2	1.2
12	48	74	18.3	51	74	13.8	−3	0	4.5
1	75	65	15.0	75	70	16.4	0	−5	−1.4

these abandoned fields prior to 5 to 10 years after the establishment of the pine.

Perhaps the 5- to 10-year-old pine stand provided a good habitat for certain birds (e.g., bobwhite quail) and these birds were responsible for seeding the sweetgum.

The measurements on the type 2 stands indicate that the presence of sweetgum in the overstory was in no case traceable to an earlier start than the pine. Apparently sweetgum was able to maintain height growth comparable to that of pine when it and the pine originated at the same time (Table 12). In almost all instances, however, the pine made more diameter growth than did the sweetgum.

These results are in agreement with those obtained by other workers. Billings (1938) noted that sweetgum in local old-field stands grew fast enough to maintain codominance with pine throughout early succession. Ralston (1951), who measured the height of three dominant trees of both species occurring on 25 quarter-acre plots in Wake County, North Carolina, found that their height growth was of the same magnitude on most upland sites, except well-drained ridges or upper slopes where loblolly outgrew sweetgum. On the uplands of southern Arkansas and Louisiana, Chapman (1942) followed the growth of 16- to 18-year-old loblolly and sweetgum trees for 6 years. He found the growth of sweetgum to be approximately equal to that of loblolly pine, both in height and diameter, when it originated at the same time as the pine.

In general, it seems that sweetgum and loblolly pine, on most upland old-field sites, have similar rates of height growth. As a consequence, height growth would appear to be of little importance in determining which of the two species becomes dominant in the first arboreal stage of upland old-field succession.

GENERAL DISCUSSION

It has been the custom in the Piedmont of the southeastern United States to clear forest land, to farm it for a number of years, and finally to abandon it. Abandonment creates an ecological void and with the processes of migration, ecesis, competition, and reaction, secondary succession is soon initiated.

In the North Carolina Piedmont many upland fields are invaded by loblolly pine, which subsequently forms the first arborescent stage leading to the ultimate climax, oak-hickory. Hardwoods rarely form the first arboreal stage on upland old-fields. This is difficult to understand since some hardwoods appear to be quite suitable to fill the role of first arboreal dominants in upland old-field succession. Sweetgum, a fast-growing species, seems to be particularly fitted for this role. It has a light, wind-borne seed, a wide ecological amplitude, and it is very common on the Piedmont uplands in pine-hardwood stands and as an understory tree in pine stands.

The purpose of this study was to determine why loblolly pine rather than sweetgum is prominent as the first arboreal dominant in upland old-field succession.

It was assumed that the role of either species is dependent on two things: the number of seeds reaching the abandoned fields, and the relative fitness of each species to germinate, to survive, and to maintain dominance while growing to maturity under old-field conditions.

The major effort was directed toward determining, in part, the relative fitness of each species for the old-field habitat. However, pertinent observations were made on the relative frequency of seed sources of each species, and on their modes of development.

The Relative Fitness of Loblolly Pine and Sweetgum for Invasion of and Growth in Abandoned Upland Fields

The widespread occurrence of loblolly pine on abandoned fields is evidence that it is able to tolerate conditions existing there. The scattered occurrence of dense sweetgum reproduction on a wide variety of sites indicates that it is also able to tolerate old-field conditions.

Yet it appeared from certain fields that sweetgum is more restricted in its reproduction than is loblolly pine. This was shown in instances where loblolly pine seedlings had become established, more or less uniformly, over entire fields, while sweetgum seedlings were limited to ditch banks or moist spots within the fields. In these situations, seed source could not have been the controlling factor. Apparently pine, because of its wider tolerance, was able to become established throughout the entire field; while

sweetgum, with its narrower tolerance, was limited to certain moist areas.

The evidence gathered from experiments on germination and survival gave support to this view.

It was found that germinating loblolly seeds are less susceptible to injury due to drying than are germinating seeds of sweetgum. Drying for 48 hours at a humidity of 45% to 55% (21°C) reduced the numbers of successfully germinating sweetgum seeds approximately 34%, while not at all affecting the amount of loblolly pine germination.

This could be a major cause for the failure of sweetgum to invade abandoned fields more frequently, especially fields with large areas of bare soil or with sparse vegetation. Such fields would be subject to rapid moisture fluctuations of the soil surface (Russel 1939; Smith 1951).

There is evidence that drying during the pregermination period might also reduce the total germination of sweetgum seed. Toumey & Durland (1923) found that sweetgum seed gave 83% germination after 20 days of soaking. Other seed from the same lot, stored in a dry condition, gave only 22% germination. Although 41% of the seed remained viable at the end of 50 days, the prospect of its germination was unlikely, since the rate of germination during the final 10 days was practically nil. In contrast, MacKinney & McQuilken (1936) showed that although dry storage slowed the rate of germination of loblolly seeds, it had little effect on the total amount.

Consideration must also be given to the rapid germination of sweetgum seed after it has been properly stratified. Evidently sweetgum seed, under favorable conditions, will germinate "en masse" in 10 to 30 days (Toumey & Durland 1923; Anon. 1948). It was reported (Anon. 1948) that 50% of the seed sown outside in January and February in a southern state germinated in twenty days. In contrast, the bulk of loblolly pine seed, under natural conditions, takes much longer to germinate (MacKinney & McQuilken 1938; Toumey & Neethling 1923; Anon. 1948). Since maximum germination rates may be expected relatively early on unshaded areas (Duncan 1951; Smith 1951), it is possible that sweetgum seed lying in newly abandoned fields would germinate during the first short spell of warm weather, only to have the resulting seedlings killed by frost. Sweetgum seed lying on cooler, shaded sites (under dense broomsedge or pine) and the more slowly germinating loblolly seed probably would remain ungerminated.

First-year seedlings of loblolly pine were found to have a relatively greater drought endurance than similarly-aged sweetgum seedlings. This was demonstrated with potted seedlings of both species, which were subjected to various periods of soil drought. Loblolly seedlings, from 39 to 163 day-old, showed a superior endurance to soil drought in every instance.

Similar results were obtained when 54-day-old seedlings of both species growing in abandoned fields were subject to a spring drought. The survival of both species varied with soils and soil moisture, but on any one soil group the survival of pine exceeded that of sweetgum. It was four times greater on light soils where drought conditions reached a maximum, twice as great on medium soils, and one-third greater on heavy soils where drought conditions were late to develop.

Since soil drought is one of the principal factors controlling the establishment of pine (Barrett 1940; McQuilken 1940; Chapman 1942), it must be doubly important as a limiting factor in the establishment of sweetgum, particularly on fields subject to frequent drought because of soils or topography.

First-year loblolly seedlings had a greater tolerance than sweetgum seedlings to summer conditions on bare or sparsely vegetated areas. On these sites, pine survival was about six times greater on light and medium soils and about three times greater on heavy soils.

Because of sweetgum's inability to tolerate conditions on bare soil, its survival during the first growing season was much greater in broomsedge. In contrast, the survival of pine was about equal on bare and on broomsedge areas. Consequently, under conditions of equal seeding of both species, loblolly would have a good chance to become established ahead of sweetgum. In some years it is probable that loblolly would be able to invade newly abandoned fields "en masse," while similar invasion by sweetgum would have to await the development of herbaceous vegetation. Additionally, the initial growth of any seedlings becoming established immediately following abandonment would be unhindered by competition from the broomsedge (Pessin 1938, found dense grass to be a serious competitor to young longleaf seedlings).

Excluding germination and survival during the first growing season, sweetgum was found to be relatively well adapted to old-field conditions.

Beginning with the second growing season, it appeared that the difference in rates of survival could be no longer considered as a factor influencing the position of either species in early old-field succession. An experiment with 2-year-old potted seedlings indicated that the drought endurance of sweetgum was at least equal to that of loblolly pine. Wenger (1952), working with 2-year-old seedlings of sweetgum, loblolly, and shortleaf pine, obtained similar results. He found that there was no statistical difference in mortality between species when seedlings growing in coarse or fine textured soils were subjected to various degrees of drought.

Field observations indicated that the survival of both species greatly increased with age. In sweetgum, part of the increase was undoubtedly associated with the development of a taproot. Probably once the roots of either species become established in the relatively root-free subsurface soil of abandoned fields, survival is no longer a problem until the forest stand closes and competition for light and water begins.

Old-field light conditions are very suitable for the photosynthesis of both species (Kozlowski 1949; see Section I). Probably, under the low competitive con-

ditions of abandoned fields, each species attains its highest possible growth rate on the uplands.

A comparison of the photosynthetic rate of both species at various soil moisture levels between field capacity and the wilting percentage revealed that sweetgum was able to maintain a higher percentage of maximum photosynthesis at the lower moisture levels. Consequently, after stand closure takes place and competition for soil moisture begins, sweetgum probably would be able to maintain its growth rate in proportion to that of pine.

Height and age measurements made on trees occurring together in stands originating on old-fields indicate that the rates of height growth of the two species are similar. Apparently, if seedlings of both species originated at about the same time in an old-field, they would, on most sites, make about the same amount of height growth. In no stands did the measurements reveal an instance of suppression of one species by the other of the same age.

The similarity in the growth habits of the two species minimizes the possibility that loblolly pine, under conditions of equal establishment with sweetgum, could dominate old-field stands because of superior height growth.

On the basis of the evidence presented, loblolly seems better fitted to old-field conditions than does sweetgum. The superior fitness of the pine is not traceable to better growth, but to better ability to tolerate old-field conditions during the periods of germination and first-year growth. More specifically, it is traceable to: (1) the ability of germinating loblolly seed to withstand drying; (2) the superior drought endurance of loblolly seedlings under one year of age; and (3) the ability of loblolly seedlings to withstand old-field conditions, particularly those occurring on bare or sparsely vegetated areas during the first growing season.

Under conditions of equal seeding, the operation of these factors would tend to give loblolly pine a numerical superiority over sweetgum. This, in turn, would partially account for its ascendancy over sweetgum as the first arboreal dominant in old-field succession, particularly on dry sites.

GENERAL OBSERVATIONS ON THE RELATIVE ABUNDANCE OF LOBLOLLY PINE AND SWEETGUM SEED SOURCES AND THE FACTORS CONTRIBUTING TO THEIR DEVELOPMENT

It is improbable that the demonstrated differences in germination of the seed and survival of the first-year seedlings alone could account for the overwhelming superiority of loblolly pine as the first arboreal dominant. If approximately the same amounts of seed of both species reached most fields, it seems likely that sweetgum would be more prominent than it is, especially on moist sites, and particularly since exceptionally wet seasons would nullify the demonstrated differences.

However, it seems that even approximately equal numbers of seeds of the two species rarely reach most abandoned fields.

From general observation, it appears that upland loblolly seed sources are much more numerous than those of upland sweetgum. This is in general agreement with the findings of the Forest Survey of 1937 (Cruikshank 1940). These results indicate that three-quarters of the five million acres of North Carolina Piedmont forest were in pine types (i.e., stands where shortleaf, loblolly, or Virginia pine make up 25% or more of the dominant or codominant stems). The loblolly pine-hardwood type which occupies a belt of land about thirty miles wide along the eastern Piedmont (including the southern half of Durham County) contained 639,000 acres of forest land. Three-fifths of this area was estimated to be in practically pure stands of loblolly pine. The remaining two-fifths was forested by a mixture of hardwoods and loblolly pine, of which loblolly made up 70.3% and sweetgum 5.6%.

In general, scattered trees of both species are found almost everywhere but, judging by McQuilken's (1940) criteria, these could not be adequate seed sources for prompt and efficient restocking of abandoned fields. Although many sweetgum occur as understory trees in pine forests, they are poor seed trees since the best seed production occurs in full light (Trenk 1929) and because, as understory trees, they are not subject to the full disseminating force of the wind.

Thus it appears that many more loblolly than sweetgum seeds reach abandoned fields. This, coupled with loblolly's superior fitness to old-field conditions, probably accounts for its overwhelming superiority as the first arboreal dominant in old-field succession. As long as a large number of fields continue to be abandoned, it seems that loblolly will maintain its present predominant position.

Diagrammatically the situation for both species would be expressed as follows:

↗ Many loblolly seed reach most abandoned fields (X) greater fitness of seed and seedlings to old-field conditions. ↘

Development of extensive seed sources. ← First arboreal dominant on many abandoned fields.

↗ Few sweetgum seeds reach most abandoned fields (X) lesser fitness of seed and seedlings to old-field conditions. ↘

Poorly developed seed sources. ← Rarely the first arboreal dominant, however important as understory tree due to continuous seeding.

The basic question remains as to why loblolly, rather than sweetgum, developed extensive seed sources in the first place.

The present distribution of seed trees might be attributed, in part, to the difference in fitness of the two species to old-field conditions. This difference, operating through many generations of abandoned

fields, could have gradually built up loblolly seed sources and relatively decreased sweetgum seed sources.

Field observations indicate that the relatively early seed-bearing age of loblolly pine probably was also of importance in the development of the present distribution of seed sources. Very young loblolly can bear viable seed (9 years—Weddell, 1935; 10 years—nurserymen, U.S.D.A. Nursery, Clayton, N. C.; 12 years—field observation), but sweetgum seed production takes several years longer (20 years—Trenk, 1929; 20 years—Anon., 1948). Because loblolly can produce seed before sweetgum, the effectiveness of young pine stands as seed sources is increased. Secondly, and most important, loblolly is able to take over many understocked areas through secondary invasion by seedlings resulting from seed produced by the initial invaders (aggregation).

Generally, very large abandoned fields, regardless of seed source, and many small fields with inadequate seed sources are poorly stocked. Understocking of the larger fields results in part because of the limited range of effective seed dispersal of most trees. This is shown by the following estimates of effective seed dispersal made by different workers for various species.

ESTIMATES OF EFFECTIVE SEED DISPERSAL

Source	*Species*	*Range of seed dispersal*
Chittenden (1906)	Sweetgum	Several hundred feet
Bryant (1909)	Longleaf pine	Height of tree (effective seeding)
Buttrick (1914)	Longleaf pine	Height of tree (effective seeding)
Hoffman (1918)	Western white pine	150 ft. (dependable reproduction)
Hoffman (1918)	Douglas fir	300 ft. (dependable reproduction)
Mattoon (1925)	Longleaf pine	1 or 2 times the height of seed tree
McQuilken (1940)	Loblolly pine	330 ft. (1000 seedlings/acre)
Wahlenburg (1946)	Longleaf pine	150 ft. (effective seeding)
Pomeroy & Korstian (1949)	Loblolly pine	200 ft. (fully stocked stand)
Table I	Sweetgum	200 ft. (2500 seedlings/acre)

Thus, even when a good seed source is present, adequate reproduction in a large field is limited to an area nearest to the seed source, while the remainder of the field is understocked. Full stocking may take place through a process of gradual seeding from the seed source, but in many instances parts of large fields are apt to remain understocked for many years following abandonment (McQuilken 1940).

On fields that receive inadequate amounts of seed, widely spaced, uneven-aged stands composed of several species frequently develop (Fig. 10). Many of these stands, regardless of the species composition, are invaded by seedlings resulting from seed produced by loblolly pines that were among the first invaders (secondary invasions by pine have been reported by Coile 1940, McQuilken 1940). In this way, loblolly is able to take over fields before other species can produce seed themselves or before sufficient seed is received from outside seed sources. In many loblolly stands, the presence of wolf trees is probably an indication of the operation of this process in the past.

FIG. 10. A field abandoned for seventeen years supporting a poorly stocked, uneven-aged mixed stand resulting from an inadequate and intermittent seed supply.

CONCLUSION

Pine generally forms the first arboreal dominant in upland old-field succession, while hardwoods hardly ever occupy this successional position. Some workers have attributed the predominance of pine to the mobility of its seed and/or the preponderance of its seed sources. Others maintain that pine occupies its position because of its superior adaptability to old-field conditions.

On the basis of this study of various phases of the life histories of loblolly pine and sweetgum, it seems that a blending of these two points of view is necessary.

Superior adaptability alone is not the single cause for loblolly's position in old-field succession. It was demonstrated that pine seeds and seedlings are better fitted to old-field conditions than those of sweetgum. However, this difference does not appear to be of sufficient magnitude to account for loblolly's overwhelming superiority as the first arboreal dominant, particularly since very wet seasons would tend to nullify the demonstrated difference. If nearly equal numbers of seed of both species reached old-fields, sweetgum probably would be more prominent than it is in old-field succession.

However, the effect of the superior adaptability of pine to old-field conditions has been magnified through many cycles of abandonment and reforestation, with a resulting gradual increase in loblolly seed sources. Additionally, the early seed-bearing age of loblolly has enabled it to take over many understocked areas through aggregation. Both of these processes probably have resulted in the build-up of the present large loblolly seed sources. These seed sources combined

with adaptability of seed and seedlings to old-field conditions apparently insure the present position of loblolly pine as the first arboreal dominant.

Sweetgum seed and seedlings, compared to pine, are poorly adapted to old-field conditions. Moreover, its later seed-bearing age reduces the possibility of its expansion in understocked fields through aggregation. Therefore, it has not developed adequately competitive seed sources and thus it is limited to a relatively minor role as the first arboreal dominant in upland old-field succession.

SUMMARY

1. In the North Carolina Piedmont, pine generally forms the first arborescent stage in upland old-field succession. Although some hardwoods seem to be fitted for this role, they rarely appear as first arboreal dominants.
2. The purpose of this study was to determine why pines rather than hardwoods are prominent as first arboreal dominants.
3. The study was limited to two representative species: loblolly pine, a common old-field tree, and sweetgum, a hardwood which seemed to have a good potential for invading old-fields.
4. Experimental and observational comparisons were made between the two species as follows:
   (a) Photosynthetic reaction under various light intensities, and under various soil moisture conditions at one light intensity.
   (b) The effect of drying on germinating seed.
   (c) The survival of one and two-year-old seedlings under various conditions.
   (d) Height growth under old-field conditions.
5. The data on photosynthesis, height growth, and survival of 2-year-old seedlings could in no way account for the presence or absence of either species as old-field dominants.
6. Observations of germination and survival indicate that loblolly pine is better fitted than sweetgum to old-field conditions because of:
   (a) The ability of germinating loblolly seed to withstand drying.
   (b) The superior drought endurance of loblolly seedlings under one year of age.
   (c) The ability of loblolly seedlings to withstand old-field conditions, particularly those on bare or sparsely vegetated areas during the first growing season.
   The operation of these factors would account, in part, for loblolly's ascendancy over sweetgum. However, if equal numbers of seeds of both species reached old-fields, the difference between species does not appear to be of sufficient magnitude to account completely for loblolly's overwhelming superiority as the first arboreal dominant.
7. On the basis of field observations of seed sources, it seems that many more loblolly than sweetgum seed reach abandoned fields. This, combined with loblolly's superior fitness to old-field conditions, could account for loblolly's great superiority as the first arboreal dominant in old-field succession.
8. The question, then, of why loblolly, rather than sweetgum, developed extensive seed sources in the first place remains unanswered. But, at least two contributing causes suggest themselves:
   (a) Its superior adaptability to old-field conditions (survival) has been magnified through many cycles of abandonment and reforestation, with a resulting gradual increase in seed sources.
   (b) The early age at which loblolly bears seed has enabled it to take over many understocked fields through aggregation.
9. On the contrary, sweetgum does not have extensive upland seed sources because:
   (a) Its seed and seedlings are poorly adapted to old-field conditions.
   (b) Its later seed-bearing age reduces the possibility of its expansion in understocked fields through aggregation.
   Because it is unable to build adequate seed sources, it is limited to a relatively minor role as the first arboreal dominant in upland old-field succession.

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THE VEGETATION OF JAMAICA

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INTRODUCTION

Plant ecology in the Caribbean has scarcely entered the broad phase of general descriptive accounts and the stage of intensive local analysis and experimental approach has not yet been reached. This is only to be expected since there are few ecologists available and often the taxonomy of whole floras is incomplete. The first step, then, is often one of descriptive phytogeography.

A number of the Central American Republics either possess recent floras or have been briefly covered in ecological papers, for example those of Miranda & Sharpe (1950), Standley (1941), Stevenson (1942) and Steyermark (1950). A general account of the area may be obtained from contributions to "Plants and Plant Science in Latin America" (Verdoorn 1945).

Of the West Indian Islands, Trinidad and Tobago have been described by Beard (1944a, 1946) but, geographically and botanically, they belong to the mainland (Venezuela). The same author (1949) covered the Lesser Antilles while the French Islands (Guadeloupe and dependencies) had already received attention by Stehlé (1935-1945). Howard (1952) has given an account of the vegetation of the Grenadines.

Turning to the Greater Antilles which form a unit of closer affinities, the plant life of Cuba has received attention from Marie-Victorin & Leon (1942), Leon (1946), Leon & Alain (1951), Carabia (1943, 1945a), and Seifriz (1943).

Porto Rico forms the subject of a complete scientific survey to which Britton & Wilson (1923-1926) contributed the flora and Gleason & Cook (1927) the plant ecology.

Hispaniola, including Haiti and Dominican Republic, appears virtually neglected except for the short report by Holdridge (Verdoorn 1945).

Jamaica, which forms the subject of the present paper, has received only sporadic and localized study. It is obvious that a more complete evaluation of the vegetation of Jamaica is long over-due. The establishment of the new University College of the

West Indies has now added a further incentive as well as being a centre for such studies.

In Jamaica, as indeed in the whole of the West Indies, there are two major aspects to be studied; the flora and the plant communities. It is under these headings that the present study is presented. While primarily concerned with describing the vegetation of Jamaica as such, some attempt is made to fit the various aspects into the whole Caribbean field by discussing the plant geographical and ecological affinities.

The ecological aspects are presented on a broad physiognomic basis and, whilst a detailed investigation of Jamaican vegetation cannot be claimed, the units described should form a sound and well-defined framework for future ecological studies of a more intensive nature. Where possible, such future lines of research have been suggested.

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GENERAL DESCRIPTION OF JAMAICA

Lying in the tropical zone some 18 degrees north of the equator, Jamaica forms part of the string of Caribbean Islands stretching in an arc from Florida to Venezuela. It is the largest of the British West Indian Islands, being 144 mi (231 km) in length running from east to west, and some 30-40 mi (48-64 km) wide. It has an area of 4,411 sq mi (11,740 sq km). With Cuba, Hispaniola (Haiti and the Dominican Republic) and Porto Rico, Jamaica forms

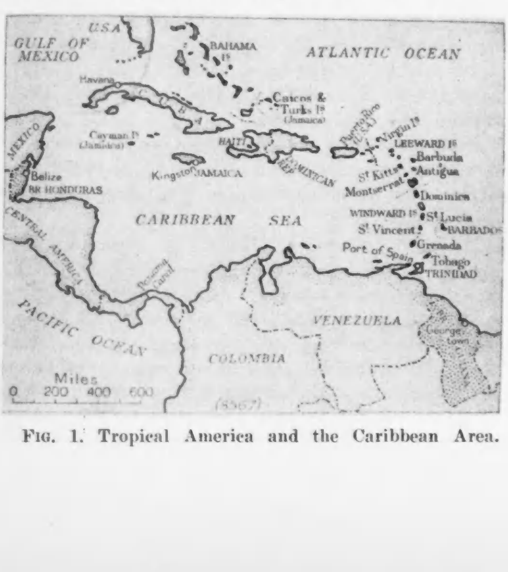


Fig. 1. Tropical America and the Caribbean Area.

a natural group of islands known as the Greater Antilles (Fig. 1).

The island is dominated by its mountains which reach their maximum height of 7,402 ft. (2,256 m) at Blue Mountain Peak. More than half of the country is above 1,000 ft. in elevation (Fig. 2). The greater part of this area is taken up by the central upland plateaus at 2,000-3,000 ft., and the Blue Mountain range in the east. In the south, the low-lying coastal fringe includes broad, flat, alluvial plains.

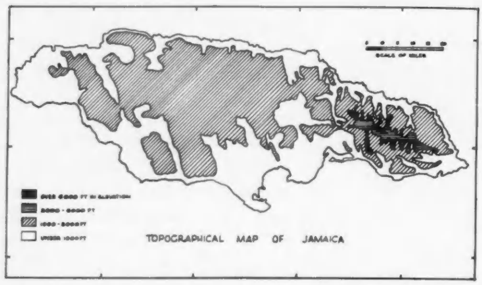


Fig. 2. Topographical regions of Jamaica. The Blue Mountain Range in the east reaches a height of 7,402 ft.

History and Land Settlement

Four hundred years of European occupation have wrought a tremendous change in the vegetation. Forests now only occur in the wet limestone country of the interior, the higher elevations of the Blue Mountains in the east, the dry limestone hills and the mangrove swamps (Fig. 3).

Occupied by the British in 1665, there followed a period of agricultural expansion which was intensified during the sugar boom of the 18th. century. The lowlands were cleared for sugar cane and the slaves given cultivation rights on marginal lands and foothills. Seasonal burning by temporary tenants for their shifting patchwork cultivation has reduced much of the forest land to a state of second growth scrub, locally known as ruinate. In early colonial times, mahogany was exported in large quantities followed by such cabinet and dye woods as fustic (*Chlorophora tinctoria*), satinwood (*Zanthoxylum flavum*), sandalwood (*Amyris balsamifera*) and lignum vitae (*Guaiacum officinale*). Today, Jamaica provides but a fraction of its own lumber requirements. Early logging methods had no regard to conservation and appalling forest destruction has been wrought by the removal of bark from valuable trees for such minor products as dye chips and tannin.

Jamaica now has 18% of land area in forests and 47% in agricultural use. The remainder, 35%, consists of second growth scrub (ruinate), thorn scrub, mangrove swamp and so on. Of the agricultural areas, 8% can be classified as tree crops (cocoa, coffee, pimento, citrus, coconuts and bananas) and 39% as food crops, plantation crops (sugar and rice) and pasture. (Summarized from returns to F.A.O. 1951.)

FIG. 3. Vegetation map of Jamaica showing the distribution of forests and major plantation crops. Place names mentioned in the text are also included; the parishes are underlined.

GEOLOGY AND SOILS

The geological history of Jamaica began in upper Cretaceous times when volcanic activity occurred. This was probably submarine as the volcanic tuffs and lavas, the Trappean Series (Sawkins 1869) are interbedded with shallow-water, marine shales and reef limestones. At the end of the Cretaceous period, uplift converted Jamaica into land. Pronounced earth-movements with folding, thrusting and faulting, accompanied the uplift and continued into lower Eocene times but had ceased by middle Eocene. During Eocene times, gradual subsidence supervened and, by middle Eocene, large areas of the island were submerged beneath a shallow sea. The sea extended progressively until, by the Oligocene, probably the whole island was submerged. Renewed uplift began in the lower Miocene but probably no land appeared until the middle Miocene when there was considerable uplift so that only the margins of the present island remained beneath the sea. This uplift was accompanied by renewed folding and faulting on a less pronounced scale, with localized exceptions where folding was intense. Later, uplift brought the island to its present form.

Broadly speaking, Jamaica has an igneous and metamorphic core, covered, for the greater part, by a limestone mantle deposited during several marine submergences. The surface consists of approximately two-thirds limestone with the other third of igneous rock, sedimentary shales and alluvium.

Hard white limestone up to 2,000 ft. thick forms some three-quarters of the surface rock and may reach an elevation of 3,000 ft. Softer yellow limestone and marl occur in some areas and are often present as a narrow bordering strip around shale areas.

Soil-forming processes and erosion are active in Jamaica. On the one hand, there is natural geological erosion and weathering associated with the relatively youthful topography of the island. These factors are still active and have produced the sharp ridge topography characteristic of the shale hills of St. Andrew. On the other hand, there is the steady loss of topsoil by leaching and erosion brought about by man's activities. Jamaica shares this common problem with other tropical countries where agriculture has been established on previous forest lands. Erosion is amplified by the steep topography, high temperature and torrential rains. Where the forest is left intact, an equilibrium is established and the soil type remains more or less stable. Due to slope and the porosity of the soil, drainage is rapid but the forest cover, so long as it protects the profile, remains. Once the forest cover is removed, however, steady leaching begins in the upper horizons with loss of nutrients. Exposure brings further erosion and often the whole of the upper horizon is missing, leaving a truncated profile. Here, cultivation is literally carried out on the lower horizons of weathering parent rock. Indeed, it may not be an overstatement that, in many parts of Jamaica, the soils approximate very nearly to the underlying geological rock pattern because of these facts. The condition is particularly prevalent in the shale areas. The eroded material is no longer deposited in valleys or flood plains but scoured out to sea during the sudden rainy seasons by swollen rivers passing through narrow valleys.

The major soil types of Jamaica will be described

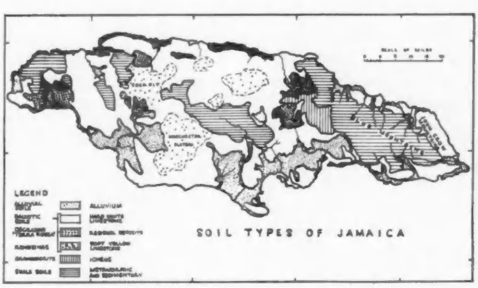


FIG. 4. The distribution of the major soil types of Jamaica and the geological formation from which they have been derived.

under three headings: Soils of the Highlands, Soils of the Upland Plateaus and Soils of the Alluvial Plains. Their distribution is shown in Fig. 4.

SOILS OF THE HIGHLANDS

In Jamaica, the highlands are made up of ancient, acid, igneous and volcanic rocks, the greater part of which are above 3,000 ft., and form the shale areas, the most notable being the Blue Mountains. The soils which may be called lithosols are very young so that they can be classified according to the type of geological formation. Their porosity is great so that leaching is heavy, leading to acid conditions and a paucity of nutrients. Under forest conditions, a high organic content is built up in the surface layers and a soil profile is developed of which the following is typical: The first 6 in. consists of a dark brown, gravelly, sandy loam. This horizon is missing when the forest is denuded. From 6-33", a dark brown, sandy, gravelly loam with a high percentage of gravel. The latter increases until solid rock is reached.

Of more sporadic occurrence, are clays produced by the weathering of fine-grained, sedimentary rocks. Drainage here is poor and, on the whole, the soils are less acid. Here the first 15" consists of dark-brown, clay loam, richly stained with humus. This overlies a yellow-red, gravelly, sandy clay loam which may extend to a depth of 40" or more and gives way to a lighter, gravelly loam and finally to the weathered parent Richmond shale.

Both types of soil are liable to rapid surface erosion following removal of the forest, leading to a truncated profile with very little other than subsoil which is extremely poor in nutrients. Such soils may be found in both the western and central shale areas. The igneous area shown on the map is composed of granodiorite and reaches an elevation of 1,500 ft. Clearing of the original forest vegetation has led to rapid erosion and the surface is now comprised of rotten rock debris, low in available nutrients and extremely porous.

SOILS OF THE UPLAND PLATEAUS

These soils are derived from limestone and fall into two categories: Terra Rossa or Red Limestone Soils and Rendzinas or Black Marl Soils.

Terra Rossa is the name applied to the residual bauxitic soils which occur mainly on the upland plateaus of Manchester and St. Ann at an elevation of 2,000-3,000 ft. They are developed from the weathering of hard white limestone through solution and are typically coarse and porous in texture. Although under conditions of poor drainage, degraded forms of these bauxitic soils occur, they are usually much leached, acid, well oxidised and dehydrated. The red colour is due to ferric oxide and their depth over the limestone plateaus varies greatly. There is no distinctive profile but the surface has a high content of organic matter on which the agricultural value of the land depends.

The black marl soils or rendzinas are developed over soft, yellow limestones and marls. Such soils are of sporadic occurrence. They develop a typical, mature profile in which the A horizon (0-6") is a heavy black or brown clay followed by a transitional zone (6-12") leading to a B horizon of light brown or yellow calcareous clay. This layer finally grades into the parent material. The soil is fine and heavy with poor drainage. High calcium status and wetness prevents development of the red colour typical of the bauxitic soils. Phosphorous is firmly bound but potash is adequate and available.

SOILS OF THE ALLUVIAL PLAINS

These soils are found on the extensive, southern, coastal plains. They have been deposited by rivers on the low-shelving coast, and are made up of loam, sand and gravel. Areas also occur where the surface alluvium is of marine origin. Here, heavy clays from 3-4 ft. deep, have been deposited over the normal riverine alluvium. The most useful agricultural land in Jamaica is found on the alluvial plains. For further information on the soils of the Caribbean, reference should be made to Hardy (1945).

Climate

Lying 18½ degrees north of the equator, Jamaica is in the tropical zone. Climatic conditions are typical of a Caribbean island with a rainy, windward coast, a dry leeward coast and a cool, central, montane region. Local climate is insular with changes in land and sea breezes during the day and night and an equable temperature throughout the year.

Due to the varying altitude from sea-level to over 7,000 ft., in the eastern end, there is a wide difference in mean temperature amounting to 23°F. The mean annual, average temperature at Kingston on the dry, south coast is 79°F and, on Blue Mt. Peak, 56°F. Generally, the coast has a greater range (17°F) than the elevated inland (12°F at 5,000 ft.). Kingston has the coolest month in February (aver. 75.7°F) and the hottest month in July (aver. 81.4°F). The highest maximum is 97.8°F and the lowest minimum 56.7°F.

Rainfall is the most important single factor affecting the vegetation. The island lies in the path of the moisture-laden, easterly trade winds which blow consistently throughout the year. Striking first the high limestone John Crow Mountains and then the northern flanks of the Blue Mountains, they are forced upwards and cooled when excess moisture is precipitated. Hence, Portland in the north east is one of the wettest parishes with over 150 in. in contrast to the dry, southern St. Andrew parish with 35 in.

The rainfall distribution map (Fig. 5) shows that about three-quarters of the island receives an annual rainfall ranging above 60 in. Seventy year records for the island as a whole, give the average, total, annual rainfall as 77 in. during an average of 123 wet days.

A feature of the rainfall is its seasonal periodicity. The island mean shows that the wettest months are October and May. The major dry period is from January to March.

Charter (1941) and Beard (1944a) emphasize the importance of the number of months in the year in

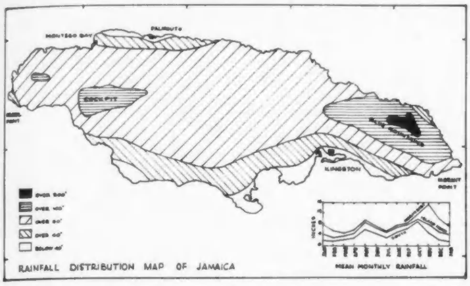


FIG. 5. Rainfall distribution in Jamaica compiled from the 70-year records. The graphs show seasonal periodicity of the rainfall resulting in maximum in May and October and a major dry period from January to March.

which excessive evaporation over precipitation leads to drought. For the Caribbean area, this point is reached with a monthly fall of less than 4 in. (100 mm) with soil of normal porosity. Seasonal distribution for Jamaica upon such a basis is given in Fig. 6.

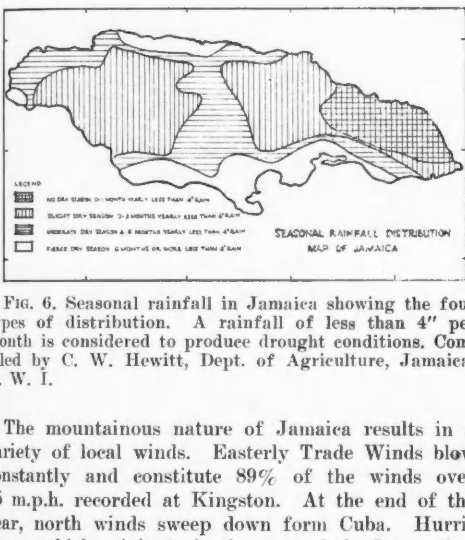


FIG. 6. Seasonal rainfall in Jamaica showing the four types of distribution. A rainfall of less than 4″ per month is considered to produce drought conditions. Compiled by C. W. Hewitt, Dept. of Agriculture, Jamaica, B. W. I.

The mountainous nature of Jamaica results in a variety of local winds. Easterly Trade Winds blow constantly and constitute 89% of the winds over 15 m.p.h. recorded at Kingston. At the end of the year, north winds sweep down form Cuba. Hurricanes, which originate in the area of the Lesser Antilles to the east, develop during August, September and October and, on the average, Jamaica may expect to be on the path of a hurricane once in 8 years.

The shortest day (Dec. 21st.) is 11 hrs., and the longest (June 21st.), 13 hours. Jamaica records 60% sunshine at Kingston compared with 33% for London. Some areas inland which are low-lying (1,000 ft.) are subject to night and early morning fogs, while the Blue Mountains have daily mists down to 3,000 ft.

FLORISTIC STUDIES

The long list of distinguished botanists that have visited Jamaica shows that the island was one of the earliest and best botanised areas in the Caribbean.

The first records of the plants of Jamaica were published by Sir Hans Sloane (1669, 1707, 1725). Then followed contributions by Brown (1756), Long (1774) Lunan (1814) and MacFadyen (1837). A flora of the British West Indies published by Grisebach (1864) remained for many years the most complete study of the island's plants. It is still an important reference point for many groups. Five volumes of the Flora of Jamaica by Fawcett & Rendle appeared over the period from 1910-1936. The monocotyledons are represented by a single volume on the orchids, while some 21 families belonging to the Metachlamydeae have still to be described. Such a brief review cannot be left without mentioning Urban's Symbolae Antillanae (1898). The location of the important Jamaica herbaria are listed by J. Lanjouw (1945). The important collection by Harris is now in the possession of the University College of the West Indies. In spite of the numerous collectors, there are still comparatively large areas unknown botanically. This has been borne out in the recent work of Proctor (1953). Working on the Pteridophytes, he has collected abundantly of species listed as rare or known only from the type specimen.

ANALYSIS OF THE FLORA

Excluding the fungi and the lichens it is estimated that Jamaica has a total flora of some 4,000 plants. Cryptogams number about 1,500 (algae 350,.bryophytes 600, pteridophytes 525). Phanerogams are just over 2,500 divided up as follows: gymnosperms 5, angiosperms 2,500 with 600 monocotyledons and 1,900 dicotyledons.

The monocotyledons number about 29 families and 213 genera with 600 species. The orchids and grasses alone account for about 400 of these species. Many of the 200 odd grasses are introductions. Of the orchids, embracing 61 genera, only one genus is endemic. In all, there are 194 species (Cuba 270), 31 of which belong to the genus *Epidendrum*. Sedges are well represented in Jamaica but are in need of revision. Bromeliaceae, listed in Grisebach as 26 species, now include 66 species in 12 genera. There are 7 genera with 13 species of indigenous palms which may be compared with Cuba's 80 species. Araceae has about 15 species in 7 genera while all the other monocotyledon families are small.

Of the 76 dicotyledon orders given in Hutchinson (1926), 62 are present in Jamaica, and contain 128 families, 647 genera and 1907 species (Tables 1, 1A, & 2).

Table 1. Analysis of the Flora. Orders of Dicotyledons.

Orders	Families	Genera	Species
Annonales	1	3	14
Apocynales	2	21 & 2*	49 & 3
Aristolochiales	1	1	5
Asterales	1	50 & 9	126 & 13
Berberidales	1	2	4
Bixales	4	10	22
Boraginales	1	7	36
Cactales	1	6	15
Campanales	3	4	13
Capparidales	2 & 1	6 & 1	16 & 2
Caryophyllales	4	12	18
Celestrales	5	10	25
Chenopodiales	5	23	38
Cruciales	1	6 & 2	7 & 3
Cucurbitales	3	9 & 4	16 & 6
Cunoniales	2	2	2
Dilleniales	1	2	2
Ebenales	2	8	27
Ericales	2	3	5
Euphorbiales	1	30 & 2	111 & 8
Garryales	1	1	1
Gentianales	1	7	13
Geraniales	4	6	7
Guttiferales	3	7	14
Hamamelidales	1	1	4
Lamiales	2	26 & 3	67 & 4
Laurales	2	8	20 & 1
Leguminosae	3	50 & 16	149 & 54
Loasales	2	3	5
Loganales	2	6	14
Lythrales	2	7	19 & 4
Malpighiales	2	10 & 1	31 & 1
Malvales	1	15	69 & 9
Meliales	1	4 & 1	9 & 1
Myricales	1	1	3
Myrtales	5	33	143 & 4
Myrsinales	1	5	28
Olacales	1	2	5
Passiflorales	1	1	14 & 3
Personales	5	54 & 3	113 & 7
Piperales	3	4	55
Plantaginales	1	1	3
Polemoniales	1	2	3
Polygonales	1	3 & 1	26 & 2
Polygales	1	2	6
Primulales	2	2	2
Ranales	3	5	9
Rhamnales	2	10	15 & 2
Rhoeadales	1	2	2
Rosales	1	5 & 1	9 & 6
Rubiales	2	42 & 4	147 & 7
Rutales	3	14 & 3	33 & 10
Santalales	2	7	22
Sapindales	4	17 & 3	36 & 4
Saxifragales	1	1	1
Solanales	2	19 & 1	98 & 1
Styracales	1	1	2
Theales	3	7 & 1	16 & 1
Thymelaeales	2	6	14
Tiliales	3	13 & 1	30 & 3
Umbelliferae	2	6	21
Urticales	3	16	78

*Introductions are shown as additions. Introduced orders such as Violales, Proteales, Casuarinales, Pittosporales, Salicales are omitted.

Table 1A. Summary of the analysis of the Dicotyledons.

	Orders	Families	Genera	Species
Archichlamydeae	45	97 & 1	389 & 37	1,161 & 124
Metachlamydeae	17	31	258 & 22	746 & 35
Total	62	128 & 1	647 & 59	1,907 & 159

Table 2. Analysis of the Flora. Families of Dicotyledons. (C = Cosmopolitan, Tr = Predominantly tropical, T = Predominantly temperate).

Families	Genera	Species
Acanthaceae (Tr)	18*	35
Amarantaceae (C,Tr)	11	24
Ampelidaceae (Tr)	3	6
Anacardiaceae (Tr)	5 & 1	14 & 2
Annonaceae (Tr)	3	14
Apocynaceae (Tr)	11	26 & 1
Aquifoliaceae (C)	1	9
Araliaceae (Tr)	3	15
Aristolochiaceae (C)	1	5
Asclepiadaceae (Tr)	10 & 2	23 & 2
Balanophoraceae (Tr)	1	1
Basellaceae (Tr)	2	2
Batidaceae (Tr)	1	1
Begoniaceae (Tr)	1	6
Bignoniaceae (Tr)	8	17
Bixaceae (Tr)	1	1
Bombacaceae (Tr)	2	2
Boraginaceae (C)	7	36
Brunelliaceae	1	1
Burseraceae (Tr)	2	4
Buxaceae (Tr)	1	4
Cactaceae	6	15
Caesalpiniaceae (Tr)	7 & 4	37 & 12
Campanulaceae (C,T)	2	2
Canellaceae	2	2
Capparidaceae (Tr)	5	15 & 1
Caprifoliaceae (C)	1 & 2	3 & 2
Caricaceae	1	2
Caryophyllaceae (C,T)	6	7
Celastraceae (C,T)	6	13
Ceratophyllaceae (C)	1	1
Chenopodiaceae (C,T)	3	4
Chloranthaceae	1	2
Clethraceae	2	4
Combretaceae (Tr)	6	8 & 1
Compositae (C)	50 & 9	126 & 13
Connaraceae (Tr)	1	2
Convolvulaceae (C)	6	50
Crassulaceae	1	1
Cruciferae (C,T)	6 & 2	7 & 3
Cucurbitaceae (C,Tr)	7 & 4	8 & 6
Cunoniaceae	1	1
Cyrillaceae	1	1
Dilleniaceae (Tr)	2	2
Ebenaceae (Tr)	1	1
Erythroxylaceae (Tr)	1	5
Euphorbiaceae (C,Tr)	30 & 2	111 & 8
Ficoidaceae	2	2
Flacourtiaceae (Tr)	1	3
Garryaceae	1	1
Gentianaceae (C,T)	7	13
Geraniaceae (C)	1	1
Gesneriaceae (Tr)	10	32
Goodeniaceae	1	1
Guttiferae (Tr)	5	12
Hernandiaceae (Tr)	1	2
Hippocrateaceae (Tr)	1	1
Hydrophyllaceae	2	3
Hypericaceae (C,T)	1	1
Icacinaceae (Tr)	1	1
Labiatae (C,T)	10 & 3	27 & 4
Lacistemaceae	1	1
Lauraceae (Tr)	7	18 & 1
Lecythidaceae (Tr)	1	1
Lentibulariaceae (C)	2	3
Linaceae (C)	1	1
Loasaceae	1	1
Lobeliaceae (C,Tr)	1	10
Loganiaceae (Tr)	2	3
Loranthaceae (C,Tr)	6	21
Lythraceae (C,T)	3	8
Malpighiaceae (Tr)	9 & 1	26 & 1
Malvaceae (C,Tr)	15	69 & 9

TABLE 2. Continued.

Families	Genera	Species
Marcgraviaceae	1	2
Melastomaceae (Tr)	18	69
Meliaceae (Tr)	4 & 1	9 & 1
Menispermaceae (Tr)	2	4
Mimosaceae (Tr)	13 & 2	25 & 12
Molluginaceae (Tr)	2	3
Moraceae (Tr)	7	18
Moringaceae	0 & 1	0 & 1
Myricaceae	1	3
Myrsineae (Tr)	5	28
Myrtaceae (Tr)	6	60 & 3
Nyctaginaceae (Tr)	4	11
Nymphaeaceae	2	4
Ochnaceae (Tr)	2	5
Olacaceae (Tr)	2	5
Oleaceae	4	11
Onagraceae (C)	4	11 & 4
Oxalidaceae (C)	1	2
Papaveraceae (C)	2	2
Papilionaceae (C)	30 & 10	87 & 30
Passifloraceae (Tr)	1	14 & 3
Phytolaccaceae (Tr)	6	7
Piperaceae (Tr)	2	52
Plantaginaceae (C)	1	3
Plumbaginaceae (C)	1	1
Polygalaceae (C)	2	6
Polygonaceae (C)	3 & 1	26 & 2
Portulacaceae (C)	2	6
Primulaceae (C,T)	1	1
Quiinaceae	1	1
Ranunculaceae (C,T)	2	4
Rhamnaceae (C,T)	7	9 & 2
Rhizophoraceae (Tr)	2	5
Rosaceae (C,T)	5 & 1	9 & 6
Rubiaceae (C,Tr)	41 & 2	144 & 5
Rutaceae (Tr)	6 & 3	22 & 10
Salicaceae	0 & 1	0 & 1
Samydaceae (Tr)	6	16
Sapindaceae (Tr)	10 & 2	19 & 2
Sapotaceae (Tr)	7	26
Scrophulariaceae (C)	16 & 3	26 & 7
Simarubaceae (Tr)	6	7
Solanaceae (C)	13 & 1	48 & 1
Staphyleaceae	1	1
Sterculiaceae (Tr)	7 & 1	16 & 2
Symplocaceae	1	2
Theaceae (Tr)	4 & 1	9 & 1
Thymeliaceae (C,T)	2	3
Tiliaceae (C,T)	4	12 & 1
Tovariaceae	1	1
Turneraceae (Tr)	2	4
Ulmaceae (C,T)	2	5
Umbelliferae (C,T)	3	6
Urticaceae (C,T)	7	55
Vacciniaceae	1	1
Verbenaceae (C,Tr)	16	40
Violaceae (C,T)	0 & 1	0 & 2
Zygophyllaceae	3	3

*Introductions are shown as additions.

The largest family is Rubiaceae with 149 species (Cuba 295), the genus *Psychotria* alone accounting for some 41. The largest order is Leguminosae with 203 species. Other large families are: Compositae 136, Euphorbiaceae 119 and Papilionaceae 117.

Families with 50 species or over are: Malvaceae, Melastomaceae, Solanaceae, Myrtaceae, Urticaceae, Convolvulaceae, Piperaceae.

Families with 35 species or over are: Caesalpiniaceae, Boraginaceae, Verbenaceae, Mimosaceae, Solanaceae, Acanthaceae.

Almost half of the orders, 26, are represented by but a single family while of the 129 families in Table 2, 42 have two or less species. These figures reflect the great number of small families and genera in the flora. There are several reasons that can be suggested for this feature. Some dozen or more families are naturally small and often of restricted distribution, eg. Cyrillaceae, Clethraceae, Quiinaceae, Garryaceae, Lacistemaceae, Tovariaceae, Batidaceae and Brunelliaceae. A few, although belonging to a large family, are represented by virtue of a single wide-ranging genus (Cunoniaceae, Linaceae). Others are temperate families represented in the tropics in montane regions (Plantaginaceae Geraniaceae, Primulaceae): others, such as Staphylaceae are disjunct. Nevertheless, there still remain large tropical families of wide distribution that are barely represented in Jamaica eg. Icacinaceae, Lecthidaceae, Loasaceae, Vacciniaceae.

Notable pan-tropic families which are not represented at all are Monimiaceae, Marantaceae, Myristicaceae and Proteaceae. The last named is found in South America and extends up to Mexico but to none of the West Indies.

Table 2 shows that 48 families are considered to be cosmopolitan. Eight of these have a predominantly tropical and 19 a predominantly temperate distribution. The overall picture shows 64 tropical families out of the 129 present. Seven families have their greater affinities in the southern hemisphere—these are Cunoniaceae, Myrtaceae, Oxalidaceae, Thymeliaceae, Goodeniaceae, Canellaceae and Rutaceae while there are nine families having predominantly northern hemisphere affinities—Ulmaceae, Garryaceae, Nymphaeaceae, Papaveraceae Staphyleaceae, Geraniaceae, Rosaceae, Primulaceae and Aquifoliaceae.

PHYTOGEOGRAPHY

A list of plants with authorities mentioned in the paper, is given in the Appendix. This list does not include the marine algae or the mosses since, for these, authorities are given in the text.

The flora of Jamaica may be grouped as follows:

i. A cosmopolitan element
ii. A West Indian element
iii. An endemic element
iv. A continental element

COSMOPOLITAN ELEMENT

These are mainly pan-tropical and pan-Caribbean plants, the highest percentage of which are strand plants such as:

Batis maritima
Borrichia arborescens
Caesalpinia bonducella
Canavalia obtusifolia
Coccoloba uvifera
Euphorbia buxifolia
Heliotropium curassavicum
Ipomea pes-capri
Sesuvium portulacastrum

Sporobolus virginicus
Tournefortia gnaphaloides

Common lowland pasture and roadside weeds reflect the 400 years of European communication in the Caribbean with such plants as:

Abrus precatorius
Achyranthes indica
Amaranthus spinosus
Argemone mexicana
Asclepias curassavicum
Boerhavia scandens
Bryophyllum pinnatum
Bidens pilosa
Borreria laevis
Calotropis procera
Capsicum frutescens
Cleome spinosa
Crotalaria retusa
Desmodium supinum
Gomphrena globosa
Gynandropsis pentaphylla
Hyptis pectinata
Jatropha curcas
Lantana involucrata
Mirabilis jalapa
Mimosa pudica
Petiveria alliacea
Pisonia aculeata
Psidium guajava
Ricinus communis
Sida rhombifolia
Stachytarpheta indica
Tribulus cistoides
Turnera ulmifolia
Urena lobata
Waltheria americana

There are others too numerous to mention. Also in this category are the many introduced trees which have become thoroughly naturalized in the lowlands, i.e., Bamboo, Mango and many Leguminosae.

WEST INDIAN ELEMENT

Although this may be regarded as an element common to the Caribbean islands, there are two aspects. Firstly, there are those plants common to all the West Indies and, secondly, a Greater Antillean element more or less distinct from the Lesser Antilles. Investigation of these two groups must await fuller botanical knowledge of these islands. The West Indian element, as a whole, includes many trees of the seasonal formations:

Acacia farnesiana
Amyris balsamifera
A. elemifera
Brosimum alicastrum
Bocconia frutescens
Brya ebenus
Bucida buceras
Bursera simaruba
Canella winterana
Ceiba pentandra
Clusia rosea
Chlorophora tinctoria
Crescentia cujete
Dipholis salicifolia
Exostema caribaeum
Guaiacum officinale
Guazuma ulmifolia
Krugiodendron ferreum
Petitia domingensis
Spondias monbin
Swietenia mahogoni

There are many common genera in the wet uplands, although the species may differ in the various regions.

Brunellia comocladifolia
Clethra occidentalis
Cyrilla racemiflora
Callophyllum spp.
Guarea glabra
Homalium spp.
Hedyosmum arborea
Ilex spp.
Juniperus spp.
Laplacea spp.
Nectrandra patens
Ocotea spp.
Prunus occidentalis
Weinmannia pinnata.

ENDEMIC ELEMENT

Endemism has been over-rated in the Caribbean and, as knowledge of the flora increases, there will be a modification of the past estimates. Complete figures are as yet unavailable for Jamaica; however, Burns (1947) confining his studies to indigenous trees and shrubs, found 440 endemics out of a total of 969 species. Fawcett & Rendle record 73 endemic orchids out of a total of 194 species. If we combine these figures and assume, for the present purpose, that there are few other endemics in the total angiosperm population of 2,500 species, a figure of 20.5% is obtained which represents the lowest possible percentage of endemism in the Jamaica flora. This figure compares with Trinidad (belonging to the Venezuelan Botanical district) of 7%; the Lesser Antilles 12% and Porto Rico 13%. Data for Cuba are unavailable at present but, judging from the large number of endemics in the flora as published so far, the overall figure will probably be the highest in the Greater Antilles.

Of the Pteridophytes, which have received recent attention by Proctor (1953), there are 90 endemic species (14%) as compared with 4% in Porto Rico. The ferns do not bear out the oft-expressed view that Jamaica represents a centre of high endemism.

Local endemism will be an interesting and fruitful field of study in Jamaica as it has proved in Cuba where no less than 16 endemic genera are localized in the north-west mountains (Carabia 1943, 1945a).

CONTINENTAL ELEMENT

The flora of the Greater Antilles is predominantly Central American in origin and its analysis sketches the history of past migrations. Biogeographers have, in the past, generally agreed that migration has taken place from Central America to the Greater Antilles. This aspect will be discussed later, however, the immediate purpose being not to prove migration but to indicate the position of Jamaica in the present-day plant distribution of the area.

The Continental element can be divided into three groups having Central, North and South American affinities respectively. It seems to be agreed that the more limited northern element was already present in parts of Central America when the Greater Antilles were linked by a land connection to the mainland. The distribution of these groups shows that, in many cases, Jamaica stands in sharp contrast to the other islands of the Caribbean. Table 3 gives a preliminary list of genera and species which illustrates this point.

TABLE 3. Distribution of the Continental elements of the Flora of the Caribbean.

	Cuba	Hispaniola	Porto Rico	L. Ant.	Jamaica
NORTHERN					
Magnolia	X	X	X	0	0
Juglans	X	–	X	0	0
Fraxinus	X	–	X	0	0
Pinus caribaea	X	0	0	0	0
Pinus occidentale	X	X	0	0	0
Phyllostylon	X	X	0	0	0
Salix	X	–	0	0	0
Quercus	X	–	0	0	0
CENTRAL					
Didymopanax	X	X	X	X	0
Bombax	X	X	X	0	0
Lysiloma	X	X	X	0	0
Brosimum alicastrum	X	X	X	X	X
SOUTHERN					
Podocarpus urbani	0	0	0	X	X
Ocotea martinicensis	0	0	0	X	X
Protium attenuatum	0	0	0	X	X
Turpinia occidentale	0	0	0	X	X
Zygia latifolia	0	0	0	X	X
Sterculia caribea	0	0	0	X	X
Crataeva tapia	0	0	0	X	X
Symphonia globulifera	0	X	0	X	X
Dacryodes excelsa	0	0	X	X	0
Epidendrum (3 spp.)	0	0	0	0	X
Brassavola nodosa	0	0	0	0	X
Maxillaria rufescens	0	0	0	0	X
Cryptarrhena lunata	0	0	0	0	X
Euterpe globosa	X	X	X	X	0
Carapa guianensis	X	X	X	X	0

The northern group is illustrated by seven genera which are found in Cuba, by-pass Jamaica, yet may reach Porto Rico but not the Lesser Antilles. Proceeding eastwards, genera may be represented by fewer species. For example, there are 3 species of *Pinus* in Cuba but only one in Hispaniola. As far as is known with certainty, Fagaceae and Saliaceae reach their southern insular limit in Cuba but Phyllostylon is represented in Hispaniola. Phyllostylon is also found in South America, however, and the family Ulmaceae is represented in Jamaica by Celtis. The genus *Magnolia* which extends to Porto Rico is absent from Jamaica and the Lesser Antilles. From the ecological standpoint too, the northern element, as a whole, becomes less important as one proceeds eastwards.

The group with Central American affinities includes several species of *Didymopanax* that are common in the Greater and Lesser Antilles but the genus is not found in Jamaica. Bombax and Lysiloma are similarly situated. On the other hand, there are species such as *Brosimum alicastrum* that have a wide distribution, being present throughout the islands and also occurring in South America.

Analysis of the southern element is more complex. The distribution pattern, as illustrated, shows that there are many species which are either common to the Lesser Antilles and Jamaica or to the entire Antilles but not Jamaica. It will be convenient here to discuss this distribution from a migrational aspect.

Much of the Southern element appears to have reached the Greater Antilles via the Lesser Antilles rather than Central America although this latter route cannot be ruled out. This view is supported by the fact that floristic representation and ecological importance in centred in the Lesser Antilles and diminishes as one proceeds northwards to Jamaica. There are many examples of such plants reaching the other Greater Antilles but missing out Jamaica. Table 3, however, is more concerned with showing examples where Jamaica is alone represented. The species of *Ocotea, Protium* and *Turpinia* may be regarded as Lesser Antillean indigenous species which have reached Jamaica as waifs by sea and wind currents. Licania, common in the Lesser Antilles, does not reach the Greater Antilles. *Dacryodes excelsa,* an important dominant of Lesser Antillean rain forest associations, goes no further than Porto Rico. In a similar category is Sloanea, represented by at least 6 species in the Lesser Antilles but by one infrequent species in Jamaica. *Pterocarpus officinalis* is present in Jamaica but never forms the large swamp forests found in the Lesser Antilles. The palm, *Euterpe globosa,* and *Carapa guianensis* are examples of southern species, widespread in the Caribbean, which by-pass Jamaica but reach Central America. There are 6 South American orchid species which occur only in Jamaica of all the West Indies. Five of these have probably reached Jamaica via Central America according to the present distribution pattern. The species of *Zygia* and *Sterculia* are South American species found in the Lesser Antilles and Jamaica. Together with *Crataeva tapia,* they are disjunct species of very problematical significance.

Some southern elements, e.g. *Weinmannia pinnata,* are of wide distribution throughout tropical America and could have equally well migrated by various routes. There are others, however, which by their distribution pattern in the West Indian islands, definitely indicate an isthmus route. The genus *Clethra* is found in South America and Trinidad but is not recorded for the Lesser Antilles or Porto Rico. However, it extends up to Mexico via Panama and extends westwards to Cuba and Jamaica. *Podocarpus urbani,* also present in Central America, is confined to Jamaica and the Lesser Antilles.

Fawcett & Rendle (1910) analysing the Orchidaceae of Jamaica, found that the greatest affinity is with Cuba where 82 of the 121 cosmopolitan species are found. Fourteen species are restricted to the

two islands. Hispaniola has 29 common species and only 2 restricted to the two islands. Porto Rico, with a better-known flora, has some 40 species in common with Jamaica. Further afield, the species of orchids in common with Jamaica are:

Bahamas	10
Florida	15
Lesser Antilles	38
Trinidad	40
Central America	44
South America	48

Many of these are cosmopolitan throughout Tropical America and have little significance in geographical affinities. However, it will be seen that there is almost equal affinity with South America and Central America and this would suggest two broad migration routes—one from the south and one from the west. Before this evidence can be fully evaluated, however, it will be necessary to relate the precise numerical affinities between each of the Greater Antilles in turn.

The fern flora of Jamaica shows a relationship with both the Greater Antilles and Central America. Affinities within the Greater Antilles are, however, not so strong with Jamaica as between the other members of this group. This follows the pattern seen in the higher plants.

It will be evident then that Jamaica holds a unique floristic position in the Caribbean either by having or lacking certain species. In this connection an observation by Woodson (1940) is of interest. Dealing with the present records of distribution of the Apocynaceae, he states "not a single instance is found of a distribution common to Hispaniola and Jamaica, except in the case of species of wide distribution throughout the Greater Antilles as a whole. On the other hand, numerous instances of distributions involving Cuba and Hispaniola are found." This conclusion is further borne out when considering the distribution of *Pinus occidentalis and Podocarpus purdeanus.* The former only occurs in Cuba and Hispaniola and the latter only in south-east Cuba and Jamaica.

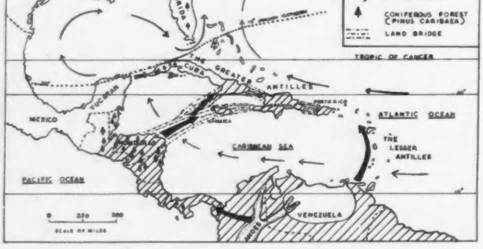


Fig. 7. Bio-geographical relations within the Caribbean. Migration to the Greater Antilles has taken place from the west by former land connections to Honduras, and from the Lesser Antilles by long-distance migration.

Until more is known of the plant ecological and floristic affinities in the Caribbean area, the examples given here must merely suggest the many problems awaiting solution. The main lines of approach must consist in careful consideration of migration methods together with the ecology of the species concerned. Broadly speaking, it would seem that the explanation of the geographical affinities of the flora of the Greater Antilles is to be found in migration from Central America by way of land connections and from the east and south by long-distance migration (Fig. 7). This will now be discussed with particular reference to the relationship of the Jamaican flora.

LAND BRIDGE HYPOTHESES

Biogeographers have postulated Central American-Antillean land bridges in at least two places, one from the Honduran peninsula to the Greater Antilles and one from the peninsula of Yucatan to Cuba. Schuchert (1935), who is the most recent authority on this subject, sees no evidence for the latter and does not believe that it ever existed. A series of diagrams representing the ideas of Schuchert on the geological history of this region are given by Woodson (1940) and are summerized in Table 4.

The important features that can be drawn from the data available are that submergences following the wide land connections during both Cretaceous and Lower Oligocene times were incomplete as far as Cuba, and possibly Hispaniola and Porto Rico, were concerned, some land remaining above the sea. After the second submergence, in the Middle Oligocene, Cuba was separated from the rest of the greater Antilles. During Upper Eocene and again in Middle Oligocene times, the southeastern tip of Cuba alone was directly connected to Honduras. In Upper Miocene times, a land connection existed between Honduras, Jamaica, Hispaniola and Porto Rico. With the exception of the centre and west of Cuba, there appears to have been no further major submergence as far as these islands were concerned, but the land bridge to Honduras was finally broken in Upper Pliocene times.

It is clear that migrations by the Antillean-Honduran land bridge will explain the broad general affinities between the floras of the Greater Antilles and Central America. Furthermore, the conjectural geographical history pointing to early isolation of Cuba, is also borne out by the presence there of such relicts as the endemic *Microcyas* and *Zamia* spp. and the high number of endemics generally, as shown in the recent flora. An explanation can also be offered of the affinity between Cuba, Hispaniola and Porto Rico, and the anomalous position of Jamaica as far as some members of the northern group of Central American plants are concerned. This could have occurred not necessarily by inter-island migration but by the continued presence in these three islands of refugia when the rest of the land, and the whole of Jamaica, was submerged. Such refugia would provide secondary centres of distribution in the islands concerned when the land, as we know it to-day,

TABLE 4. The Conjectural Land Connections of the Greater Antilles (after Schuchert 1935).

Geological Period	Land Connections	Remarks
Upper Pliocene—Pleistocene	None	Cuba submerged except for S. E.
Upper Miocene—Lower Pliocene	Honduras—Jamaica—Hispaniola—Porto Rico	Narrow separation from Cuba to N. W. Hispaniola
Lower Middle Miocene	Honduras—Jamaica—Hispaniola	Much of Cuba & Hispaniola submerged
Upper Oligocene	No connections to mainland	Cuba submerged except for south-east corner; Jamaica completely submerged
Middle Oligocene	Honduras—S. E. Cuba: Jamaica—Hispaniola: Hispaniola—Porto Rico	Cuba finally isolated from rest of Greater Antilles
Lower Oligocene	Honduras—G. Antilles—Bahamas	
Upper Eocene	Honduras—S. E. Cuba: Jamaica—Hispaniola: Hispaniola—Porto Rico	All low parts of islands submerged
Upper Cretaceous	S. America—C. America—G. Antilles—Bahamas—S. Florida	

subsequently emerged. Such a scheme would account for distribution of northern species following the Magnolia pattern and central species following the Bombax, Lysiloma pattern. It does, of course, assume that such plants had already migrated from Central America by these times. As to whether this is a reasonable assumption or not, we have no evidence. However, if they were present, the question might well be asked why did migration not take place to Jamaica from Hispaniola during the land connection of Upper Miocene times?

The only other alternative would seem to be that there may have been inter-island migration of these species which arrived in Cuba during those periods when Cuba alone was connected to Honduras. It is difficult to find any adequate reasons why Jamaica should have been left out of such migrations.

Species distributed according to the pattern of *Pinus caribaea* and the oaks which appear to be confined to Cuba, are in a different category from the above and may well be taken as an example of the danger of putting too much emphasis on land bridges alone without considering the ecological implications of the species concerned. The distribution of *Pinus caribaea* in the Caribbean area is indicated in Fig. 7. Ecologically, it is confined to a habitat where the soil consists of flat siliceous sands (which may be at sea level or up to 2,000 ft.), supporting a Pine savanna of sedge and grasses dotted with pine trees, oaks and a few characteristic associated shrubs. It is absent from Jamaica and possibly the other islands of the Antilles, because there are no habitats present with the edaphic conditions required. It should, furthermore, be noted that, at the present time, *Pinus caribaea* is confined to the west of Cuba where such soils occur. This area, according to Schuchert, was submerged as late as Upper Pliocene-Pleistocene times and it is extremely unlikely that any land present in south-east Cuba would provide a refuge for the members of this specialized community. It must be assumed, then, that *Pinus caribaea* arrived in Cuba at a later date and it is tempting to suggest that this was via a land-bridge extending from Yucatan to Cuba, 160 mi away.

It is generally agreed that no land-bridge ever existed between Cuba and Florida and North America. Southward, a continuous land-bridge has been postulated through the Lesser Antilles to South America. This is very doubtful owing to the differing age and volcanic origin of these smaller islands. Beard (1948) has shown that the past geologic history of the Lesser Antilles is reflected in the flora which supports the view that these islands were never linked by a land-bridge.

LONG DISTANCE MIGRATION

Within the Caribbean as a whole, emphasis has been upon continuous land connections. Long distance migration has been relegated to a minor role. Nevertheless, there is much evidence that migration of plants with wind-borne dissemules, has occurred. Strong winds blow down from Cuba to Jamaica in the months of November and December. This may account for the affinity between these two islands of the Orchidaceae and the Pteridophytes. Furthermore, sea and wind currents, often of hurricane force, pass upwards from the Lesser Antilles to the Greater Antilles and the Caribbean shores of Central America for most of the year. Dealing with the distribution of the Apocynaceae, Woodson gives evidence supporting the assumption that wind-borne seeds account for the migration of Greater Antillean species such as *Echites lutea*, *Echites umbellata* and *Rhabdadenia biflora* to the mainland of Central America. In the absence of any evidence for a land-bridge connecting the Greater and Lesser Antilles to South America, it must be assumed that many of the species in Jamaica

that have affinities with the Lesser Antilles, have arrived by long distance migration. How this has occurred should be worked out for each species in detail, bearing in mind that there are many examples, such as those of southern species given in Table 3, which are not common to the Greater Antilles as a whole. Chapman (1947) presented figures showing the geographical relationship of the seaweeds of Jamacia to Florida, the Bahamas and the Virgin Islands. These affinities are undoubtedly due to the prevailing sea currents.

The importance of birds and bats as agents for the spread of plants in the Caribbean has been stressed by Beard (1949). He estimates that at least two-thirds of the rain forest trees of the Lesser Antilles produce fruit attractive to these animals and thinks that this may account for their migration from South America.

Paleobotanical evidence for the Carribbean is fragmentary. Genera and families have been traced back to the Cretaceous and Tertiary, and there appears to have been a sudden flush of new species since that time which, no doubt, has some bearing upon the high endemism claimed for the West Indies (Hollick 1924, 1928). The Jamaican record has not been studied. A well-preserved palm type has been recently found. However, all the fossils date back to a pre-emergence period and so belong to a lost flora.

COMMUNITY STUDIES

Introduction

The vegetation of Jamaica, with the exception of the montane regions, is tropical. Typical of Caribbean islands, the major ecological boundaries are determined by a wet northern coast, a central montane region and a dry southern plain. The determining factor is rainfall which, in turn is dependent upon the prevailing wind and the mountain barriers in its path. Within these boundaries, however, many local factors operate to bring about a very diverse and varied vegetational pattern.

The vegetation as a whole has never been described. The sparse literature which exists on the subject comprises, for the most part, descriptive essays written by visiting botanists, or more intensive investigations of a single aspect. The Caribbean Commission (1947) on forest research for Jamaica reported that "no appreciable data are available on plant ecology or other aspects of forest biology" and stated that there was an urgent need for a detailed ecological survey of the forest types and successional groups.

In 1846, the Danish botanist, Ørsted, visited Jamaica and later published a map and description of the vegetation, outlining the broad plant communities. There are also some brief generalized descriptions of historical interest by Sir Hans Sloane, Browne, Swartz and other early workers. Harshberger (1903) and Shreve (1910) describe some of the coastal vegetation, while Shreve (1914) gives an account of the higher montane forest together with some physiological investigations. A lengthy paper by H. & M. Brockmann-Jerosch (1925) is remarkable if only for the fact that it was based upon a three-week visit in 1913. A cross section of the eastern (Blue Mountain) end of the island is well described from the route taken and perhaps remains as one of the best general reports to date. In 1939, Cambridge University sent a small expedition to study mangrove communities. The results were published by Chapman (1940, 1944).

Although initially the sole objective was to describe the local vegetation, it soon became evident that account must be taken of the ecological correlations necessary to fit the vegetation of Jamaica into the Caribbean area as a whole. Beard (1944a) has specifically discussed the problems of ecological classification within the Carribean and proposed a system for general use throughout Tropical America. He has already used his system to advantage in his excellent monographs on Trinidad (1946) and the Lesser Antilles (1949). An attempt to correlate the vegetation of Jamaica with the vegetation types recognized by Beard is made in the discussion (p. 403).

There are various ways of presenting the vegetation of Jamaica. Swabey (1942) proposed an outline classification which was based on that of Burtt-Davy (1938). While somewhat unwieldy, the main points may be summarized. In Jamaica, he recognized climatic and edaphic climax formations. The former included moist woodland with 70 in. of rain, dry woodland with 50 in. and montane formations. Edaphic climax formations included wet limestone woodlands, dry limestone woodlands and the maritime swamp and aquatic formations. Finally, there were a number of seral "formations". It is interesting to note that the "limestone formations" were regarded as edaphic climaxes. The simplest approach is that adopted by Gleason & Cook (1927) for the vegetation of Porto Rico where they described separately a wet northern region, a central montane and a dry southern region.

In Jamaica, however, the major headings fall more naturally under coastal, lowland and montane.

The coastal communities include the marine vegetation, communities on sand beaches, sand spits and coral rock. Under this heading too, special consideration is given to the small islands known as Cays that occur off the coast. The lowland communities are discussed under four main headings. These are limestone, alluvium, shale, and the swamps and marshes. The montane vegetation is conveniently divided into lower montane rain forest, montane sclerophyll, and montane mist forest with its elfin woodland aspect.

The method of classification is mainly one of convenience. It is based largely upon the edaphic factor. While the recognition of an edaphic climax is not advocated, it cannot be denied that soil type is an important factor in Jamaica where limestone rock and derived soils, "shale" hills and alluvial plains form the major soil patterns. It has already been emphasized how closely the soil-boundaries are correlated with the geological map. It is further remarkable how con-

veniently the rainfall and topographic maps correspond in Jamaica. Only in the John Crow Mountains is there any major deviation. Edaphic factors are also important elsewhere in the Caribbean, for example the volcanic soils of the Lesser Antilles and the serpentine and siliceous savannas of Cuba.

COASTAL COMMUNITIES

The coastline of Jamaica consists, for the most part, of limestone rock or low-fringing coral shelves. High sea cliffs and headlands are infrequent. Variation is given by the occurrence of bays with sandy spits, beaches and by alluvial deposits at river estuaries. The larger bays and sheltered estuaries are mainly on the south coast.

The south coast is drier than the north and the average rainfall is often below 30 in. (Fig. 5, 6). On the north coast, the only area which approaches this figure is that between Falmouth and Montego Bay, where the average is about 40 in.

Since the bulk of the rain falls in the two rainy seasons embracing the months of May and October, long periods of drought occur. The arid nature of this halophytic habitat is further intensified by the fierce insolation, porosity of the substratum and salt-laden winds which may reach hurricane force.

Apart from restricting the height of the vegetation, wind is an important factor in the development of marine currents which bring about deposition of rock, gravel and sand, forming the beaches, spits and cays which are eventually colonised by the strand communities.

At the river mouths and in sheltered areas, a sediment of fine silt is built up to form mud banks. These are colonised by mangroves which assist the processes of accretion and land formation by retaining the silt.

Tidal range in Jamaica is very restricted, being less than 16 in. and averaging 10 in. This is not only important to the marine vegetation but also affects the sand communities. These are confined to a narrow fringe rarely elevated more than a few feet above the sea, so that the substratum is open to modification by accretion or erosion during heavy storms and hurricanes. Strand vegetation is generally in a state of flux and the beaches and spits may show both accretion and erosion occurring simultaneously.

MARINE VEGETATION

Marine algae are not abundant around the coast of Jamaica in comparison with temperate zones. This is, no doubt, due to the small tidal fluctuation and the steeply shelving shore line. Much of the substratum is also unsuitable for the establishment of algal communities.

In shallow waters of sheltered and silty bays, the marine grasses *Thalassia testudinum* and *Cymadocea manatorum* are often abundant.

Green algae are well represented, especially the lime-encrusting members of the Siphonales such as Halimeda, Acetabularia and Cymopohlia but there is a general paucity of brown seaweeds. The red algae are chiefly small, insignificant and epiphytic. Chapman (1947) gives the following figures:

Chlorophyceae	105
Cyanophyceae	51
Phaeophyceae	36
Rhodophyceae	135
Total	327

Zonation, which is usually associated with large tidal fluctuations together with a sloping shoreline, is virtually absent in Jamaica. The communities are seldom, if ever, uncovered by water, and the habitat groups that may be recognized are based upon protection, substratum and, to a lesser extent, depth of water.

Flat coral shelves extending from the shore line and covered by a foot or so of water together with reefs up to 10 ft. under the sea and several hundred yards off shore, provide the most frequent habitats.

In deeper water, on the seaward and exposed edges of the rocks buffeted by the waves, the following may be found:

Sargassum vulgare C.Ag.
S. lendigerum (L.) Kuetz
S. polyceratium Mont. var. *ovatum* Collins
Dictyota dentata Lamx.
Cutleria sp.
Turbinaria turbinata (L.) Kuntze
Dictyopteris delicatula Lamx.
Acanthophora spicifera (Vahl) Børgs.
Bryothamnion triquetrum (Gmel.) Howe
Gelidiopsis rigida (Vahl) Weber-van Bosse
Grateloupia filicina (Wulf) C.Ag.
Avrainvillea nigricans Decsne.
Gracilaria lacinulata (Vahl) Howe

Most of the algae are to be found on the shallow flat surface of the coral shelves. This has several aspects; the rock may be bare or covered with a layer of silt; it may be exposed, sheltered or have deeper parts where there are indentations or pools.

Caulerpa racemosa (Forsk.) Weber-van Bosse var. *uvifera* (Turner) Weber-van Bosse, grows best on the silt where it forms long rhizomes. Here, also, are to be found *Udotea flabellum* (Ellis & Solander) Howe, *Acetabularia crenulata* Lamx., *Penicillus capitatus* Lamarck and *P. pyriformis* A. & E. S. Gepp.

In quieter waters the following may occur:

Caulerpa taxifolia (Vahl) Ag.
C. cupressoides (Vahl) Ag.
Codium tomentosum (Huds.) Stackh.
Cymopolia barbata (L.) Haw.
Halimeda tuna (Ellis et Solander) Lamx.
H. opuntia (L.) Lamx.
H. incrassata (Ellis et Solander) Lamx.
Zonaria zonalis (Lamx.) Howe
Padina vickersiae Hoyt
Rhipocephalus phoenix (Ellis et Solander) Kütz.
Laurencia obtusa (Huds.) Lamx.
L. intricata Lamx.

The tidal fringe provides another habitat where the component species are just covered by water and usually of low moss-like life form. Species common here are:

Ectocarpus sp.
Chaetomorpha sp.
Microdictyon boergesenii Setchell
Valonia ventricosa J.Ag.
V. aegagrophila C.Ag.
Cladophoropsis membranaceae (Ag.) Børgs.
Polysiphonia sp.
Dictyosphaeria cavernosa (Forskul) Børgs. *favulosa* (Ag.) Decsne.
Cladophora sp.
Enteromorpha sp.
Ulva sp.

We are indebted to Prof. V. J. Chapman of Auckland University College, New Zealand for many of the determinations.

STRAND COMMUNITIES

In Jamaica, coastal communities are found on three types of substratum, viz. sand, limestone and coral rock, and mud (See Fig. 12). The last named is occupied by mangrove swamps which are described later when dealing with the swamp formations. The mangroves, although found on shallow reefs and sand banks, reach their full development along sheltered, muddy estuaries. They are subject to tidal inundation and escape the drought conditions of the land plants growing on porous sands and rocks. It is, thus, not surprising that the mangrove association is so clearly distinct from the other coastal communities. However, all share the common feature of having successional patterns involving topographical changes.

In describing the vegetation on sand and coral rock, a simple classification upon a seral basis is the most satisfactory. Davis (1942) suggested the following for the Caribbean:

i. a strand-beach associes
ii. a strand-dune associes
iii. a strand-scrub associes
iv. a strand-woodland association

He recognized these communities on the Florida Keys where they corresponded to a pioneer open community on mobile sand, an herbaceous community of the fixed dunes, a scrub community and a climax of woodland. It is under these general headings that the strand communities of Jamaica will be described.

THE STRAND-BEACH ASSOCIES

The beach sands of Jamaica are highly calcareous, containing high proportions of weathered and pulverised limestone and coral rock, together with sea shells and calcareous algae. In a few localities, the sand is predominantly of Halimeda remains. There are no coastal dunes such as seen in Porto Rico, the nearest approach being on the Palisadoes where sand has been built up over a shingle bank to a height of 20 ft.

Coastal beaches are to be distinguished from those found on the seaward side of spits. True beaches are few in number, the best examples being on the north coast where they are popular resorts and, consequently, the natural vegetation has suffered. A few are bounded by cliffs and restricted in width. Modifications have been brought about by the planting of coconuts and the proximity of the coastal roads. It is on these beaches that the best development of the pioneer phases is to be seen. On the spits, continual erosion and modification restricts this community.

This pioneer associes begins above the tidal limits on initially, and potentially, mobile sand. Salinity is high but there is adequate moisture immediately below the surface. Wind and storms may bring about local or major alterations in topography due to sand removal or accretion.

The important plants are halophytes and psammophytes with quick vegetative propagation by runners. *Ipomea pes-capri* flourishes on the mobile sand front and, together with *Sporobolus virginicus,* an important sand-binder, is invariably present in the pioneer associes. The long, trailing runners of Ipomea spread for a length of 40 ft. or more across the beach, whilst the tough, wiry rhizomes of Sporobolus bind the sand.

Other plants, abundant to frequent, are: *Euphorbia buxifolia, Sesuvium portulacastrum, Cakile lanceolata* and the grasses *Cenchrus tribuloides, Chloris petraea, Spartina patens* var. *juncea* and *Paspalum vaginatum*

The extent and development of the pioneer zone depends much upon the width and elevation of the beach as well as interference by man. On beaches where active erosion is taking place, the pioneer zone is marked only by a sparse drift-line flora fronting a hedge of Coccoloba and Thespesia (Fig. 11). Even where well developed, it is essentially a very open, successional community.

Plants of the strand-beach associes:

Sand runners and binders:
Ipomea pes-capri
Sporobolus virginicus
Cenchrus tribuloides
Paspalum vaginatum

Herbs:
Euphorbia blodgettii
E. buxifolia
E. hypericifolia
Sesuvium portulacastrum
Cakile lanceolata
Heliotropium curassavicum
Erigeron canadensis
Lippia reptans
Philoxerus vermicularis
Atriplex cristata
Manisurus altissima
Portulacca pilosa

Grasses and Sedges:
Chloris petraea
Spartina patens
Cyperus brunneus
Cenchrus pauciflorus
Uniola virgata

THE STRAND-DUNE ASSOCIES

This is the second phase in the succession and is characterized by being a closer and predominantly herbaceous community on the fixed dunes. It may emerge from the pioneer zone or, where this has been destroyed by wave action, begin sharply from the eroded shelf. This community is well represented.

The seaward fringe is usually dominated by small tussocks of Sporobolus in close formation. Intermingled with this, or forming an inner zone is *Spartina patens,* a typical psammophytic grass with rolled leaves.

Other common plants are Cenchrus, Chloris, *Cyperus brunneus, Euphorbia buxifolia, Sesuvium portulacastrum, Alternanthera ficoidea, Opuntia tuna* and, on the Palisadoes, *Tribulus cistoides.*

Occasional adventives from the scrub are found including *Scaevola plumerii, Tournefortia gnaphalodes, Suriana maritima, Borrichia arborescens, Caesalpinia bonducella.*

Wind-stunted Acacia and Coccoloba may also be present.

Sharp definition between this zone and the next is rare. More usually there is a gradual merging shown by an increase in the shrub population. Plants of the strand-dune associes:

Herbs:

Sporobolus virginicus
Spartina patens
Cenchrus tribuloides
Chloris petraea
Cyperus brunneus
C. laevigatus
C. ligularis
Hymenocallis sp.
Euphorbia buxifolia
Fimbristylis ferrugineus
F. spadicea
F. glomerata
Sesuvium portulacastrum
Philoxerus vermicularis
Alternanthera ficoidea
Canavalia obtusifolia
Opuntia tuna
Stemodia maritima
Erigeron canadensis
Eustoma exaltatum
Talinum paniculatum
Isocarpha oppositifolia
Egletes prostrata
Eragrotis ciliaris

Occasional shrubs:

Scaevola plumerii
Tournefortia gnaphalodes
Borrichia arborescens
Suriana maritima
Caesalpinia bonducella
Coccoloba uvifera
Acacia tortuosa
Spilanthes urens
Melochia crenata
Turnera ulmifolia

THE STRAND-SCRUB ASSOCIES

This associes is seldom well developed on the sand beaches due to their limited width and human interference. It is best seen on sand overlying raised coral rock shelves.

Beaches of this type are found on the north coast and here the scrub is dominated by Suriana, Tournefortia, Borrichia and Scaevola. Other frequent species are:

Caesalpinia bonducella
Ernodia littoralis
Erithralis fruticosa
Solanum havanense
Morinda royoc
M. citrifolia
Colubrina asiatica
Coccoloba uvifera
Phyllanthus epiphyllanthus

The open spits of the south coast have a different succession, the climax often being replaced by a cactus thorn-scrub related to that of the alluvial plains. Here, the strand scrub stage is most frequently made up of low, sparse, bushes of *Acacia tortuosa, Prosopis juliflora, Boerhavia scandens, Capparis ferruginea, Coccoloba uvifera, Pithecellobium unguis-cati, Jatropha gossypifolia* and cacti together with the usual grasses, sedges and halophytic herbs. The introduced *Calotropis procera* is present on the Palisadoes.

THE STRAND WOODLAND ASSOCIATION

The most frequent woodland on the strand is the Coccoloba-Thespesia association which may be seen on many beaches around the coast. Although usually exclusive, the following may also be present: *Conocarpus erecta, Dalbergia ecastaphyllum, Colubrina asiatica, Morinda citrifolia, Piscidia piscipula,* and *Sophora tomentosa.*

On the north and east coasts, particularly where there is a raised coral shelf, a characteristic strand woodland develops. This is a low (10-20 ft. tall) scrubby, open forest which may include palms and a mixture of trees and shrubs, many of which are from the arid limestone regions. Morant Point in the southeast, exposed to the full force of the easterly trade winds, supports a stunted woodland, more aptly described as "scrub" but rendered conspicuous by the presence of the palm *Thrinax parviflora* occasionally reaching a height of 25 ft. (Fig. 8). The important constituents here are:

FIG. 8. Stunted palm woodland at Morant Point. In the foreground are to be seen *Cordia sebestana* on the left and *Morinda citrifolia* in the centre. The palm is *Thrinax parviflora* and the wind-swept trees in the background are Conocarpus, Capparis and Hippomane. *Croton flavens* forms the ground layer.

Hippomane mancinella
Coccoloba uvifera
Cordia sebestana
Conocarpus erecta
Capparis ferruginea
Eugenia buxifolia
Jacquinia armillaris
Plumiera alba
Colubrina asiatica
Erithralis fruticosa

Also recorded are:

Thespesia populnea
Opuntia tuna
Machaonia rotundata
Croton linearis
C. flavens
Melochia lupulina
Ficus morantensis
Helicteres jamaicensis
Suriana maritima
Morinda royoc
M. citrifolia

On the coastal ledge near Falmouth, which may be up to 200 yd. wide and is relatively protected, the woodland is much more strongly developed. Some of the larger species such as Thespesia, Coccoloba and Lonchocarpus are up to 10 in. in trunk diameter and at least 30 ft. tall, whilst the average height of the canopy is 20-25 ft. There are no palms here but a much greater variety of species than at Morant Point. Nevertheless, it will be seen from the species lists that many are common to both these regions.

Important species occurring here are as follows:

Trees:

Pithecellobium unguis-cati
Hippomane mancinella
Coccoloba uvifera
Concarpus erecta
Thespesia populnea
Capparis ferruginea
C. cynophallophora
Eugenia sp.
Tecoma leucoxylon
Comocladia sp.
Leucaena glauca
Rhacoma crossopetalum
Gyminda latifolia
Amyris elemifera
Lonchocarpus latifolius
Peltophorum braziliense

Shrubs:

Jacquinia armillaris
Erithralis fruticosa
Randia aculeata
Helicteres jamaicensis
Melochia tomentosa
Lantana involucrata
Yucca aloifolia
Abutilon giganteum
Croton flavens
Citharexylum fruticosum

Herbs and Climbers:

Tournefortia volubilis
Tragia volubilis
Solanum havanense
Aegiphila elata
Echites umbellata
Pisonia aculeata
Opuntia tuna
Aloe sp.

Also recorded from other areas are: *Ficus aurea, Coccoloba littoralis, Clusia rosea, Clusia flava,* the scrambling shrub *Hyperbaeba domingensis,* and the palms *Sabal jamaicensis* and *Coccothrinax fragrans.*

THE SAND SPITS

Spit formation is of frequent occurrence in Jamaica and, since the subject has an important bearing upon the formation of lagoons, salt ponds, salinas and beaches, all of which determine the coastal vegetation in general, a fuller account is not out-of-place here. Spits also bear some relation to the Cays to be described in the next section.

The history of spit formation and its subsequent development is easily worked out and a series of diagrams illustrating this process has been constructed from the various examples seen around the coast (Fig. 9). Starting with an open bay, the first stage is the development of a narrow tongue stretching towards the opposite shore (Stage 1). A sheltered lagoon is produced in which mangroves appear and silt is deposited. Next, the spit is thrown completely across the bay to form a sand bar and an inner salt pond (Stage 2). Subsequently, dry land is produced by evaporation from the shallow areas silted up during the lagoon phase (Stage 3). Finally, all that remains is a beach with a fringing background of mangroves (Stage 4). Dry land formation may be accelerated by riverine deposits of silt or seismic elevation of the land proceeding at the same time.

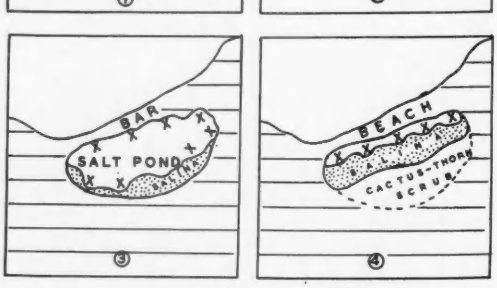


FIG. 9. Diagrams illustrating sand spit formation (1), and the subsequent development of a sand bar and a salt pond (2), followed by a salina (3). In the final stage (4), the usual strand communities are developed on a beach backed by mangrove woodland (X) and a salina that is being invaded by cactus thorn scrub.

All stages of these processes can be seen around the coast of Jamaica from the embryo spit through sand bars backed by shallow lagoons and salinas to popular bathing beaches. The only evidence of this sequence in the final beach stage is the presence of the last few remaining mangroves, marking the inner edge of the former spit.

The vegetation on the spits shows distinct zonation. On the seaward side, a pioneer zone, which may only be represented by a drift line flora containing typical pioneer species, is followed closely by a narrow dune stage. This zone leads directly into a cactus-thorn scrub in the centre of the spit. On the inner edge, mangroves are developed and may show typical zonation of species from Rhizophora in shallow water, through Avicennia and Laguncularia to Conocarpus on dry land. This is illustrated by the profile diagram in Fig. 10. That these types of zonation depend entirely upon the age, width and elevation of the spit is clearly demonstrated by the Palisadoes and the Hellshire spits. A diagrammatic representation of the Hellshire spit is also given in Fig. 10. On the narrowest and youngest region, only the pioneer stage is seen. As the spit broadens, the fixed dune stage is included and, on the inner shore, Rhizophora appears. Further widening and elevation leads to the appearance of cactus-thorn scrub which may be the final stage, as on the Palisadoes. It should be noted, however, that, at the widest and most mature end of the Hellshire spit, a zonation typical of a beach is shown and the climax is strand woodland of *Coccoloba*

FIG. 11. Strand woodland of *Coccoloba uvifera* and *Thespesia populnea* fringing the Hellshire sand spit. The strand dune zone has been removed by erosion although a remnant may be seen in the sand cliff near the figures. In the foreground is the tidal drift-line zone above which is a zone of mobile sand colonized by *Sporobolus virginicus*.

uvifera. Erosion may cause modification by entirely removing the pioneer, dune and scrub stages so that the Coccoloba woodland fringes the shore directly (Fig. 11).

A perfect example showing the sequence of communities on sand postulated by Davis for the sand keys of Florida has yet to be seen in Jamaica. Many of the more extensive sand beaches have become popular holiday resorts and the natural vegetation destroyed or markedly altered. On the south coast, the succession is modified by the invasion of thorn scrub vegetation similar to that on the alluvial plains. On the north coast, the raised coral rock shelves introduce a further complication. It is, therefore, premature at this stage to enter into the details of successional relationships. Nevertheless, the following pattern suggests itself and is illustrated in Fig. 12.

The pioneer strand beach associes is followed by the more stable strand dune associes. Further topographical and edaphic changes lead either to a climax of Coccoloba-Thespesia strand woodland or, on the sand spits of the south coast, to a climax of cactus thorn scrub. However, where the sand is built up

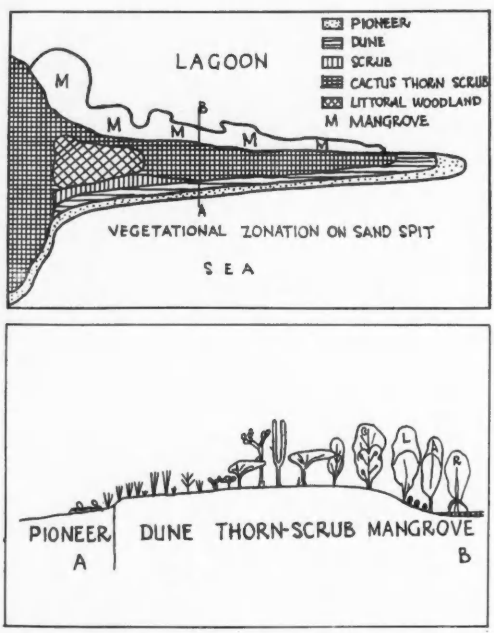


FIG. 10. Diagrammatic representation of zonation on the Hellshire sand spit. The profile is taken across the spit from A-B. Zonation depends upon the age, width and elevation of the spit.

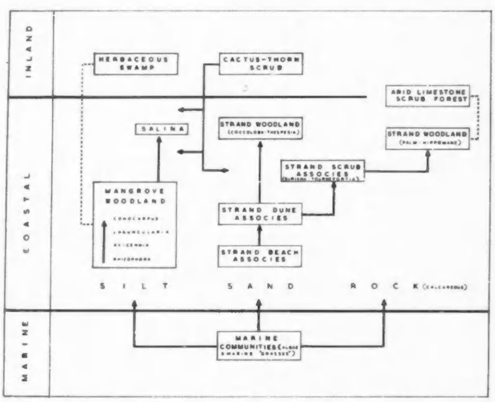


FIG. 12. Scheme illustrating the relationships between the marine, coastal and adjacent inland communities.

over coastal limestone and coral rock shelves, a different zonation appears. Proceeding inland, a poorly developed strand-dune associes gives way to the Tournefortia-Suriana strand scrub associes which, in turn, is succeeded by Palm-Hippomane strand woodland. The last two coastal communities have, so far, only been seen in Jamaica where there is a substratum of limestone on coral rock. It is interesting to note, however, that Davis found no significant difference between the rock hammocks (woodland) and the sand hammocks of the Florida keys. Whether the strand scrub and Palm-Hippomane woodland are part of the psammosere in Jamaica is doubtful. The latter community would seem to have closer affinity with the coastal fasciation of Dry Limestone woodland. Mangrove woodland develops in protected areas where silt is deposited.

LIME CAY

Fig. 13. Diagrammatic representation of the vegetation type on Lime Cay.

THE CAYS

Discussion of the vegetation of the Cays will be limited mainly to some of the Port Royal Cays visited by the Cambridge Expedition in 1939 and the authors in 1952.

A cay (or key) is a small island of sand or coral rock. The cays of Jamaica have been described by Steers, et al. (1940). Those nearest to the coast occur off the Palisadoes and in the Portland Bight. The former are called the Port Royal Cays. In addition, there are the Morant Cays, 30 mi. south-east of Morant Point, and Pedro Cays, 60 mi. south-west of Kingston. The cays are built upon exposed coral reefs in the open sea. Reef exposure is stated by Colman to be due to two causes: a fall in sea level and the formation of beach rock Beach rock develops as a result of the precipitation of calcium carbonate from sea water at the site of turbulent wave action. Sea water, rich in carbon dioxide, can dissolve calcium carbonate much more readily than normal sea water. The excess is precipitated when the carbon dioxide is removed by violent aeration. The calcium carbonate so deposited binds together the sand and rock particles immediately underneath the surface. Cay formation is initiated by the accumulation of sand in the hollows of flat reefs or behind boulders and rock fragments thrown up by storm action. The sand itself contains a high porportion of the pulverised remains of calcareous marine animals and plants, amongst which *Halimeda opuntia* is conspicuous.

Lime Cay

Lime Cay is the largest of the Port Royal group, being about 30,000 sq. yd. in area. It supports the most advanced type of vegetation. Unfortunately, it has not been surveyed but the sketch shown in Fig. 13 is a reasonably accurate representation of its structure. The cay consists of sand, containing a high proportion of the remains of the lime-encrusting *Halimeda opuntia,* which has been deposited on the leeward side of an arc-shaped reef. Members of the strand pioneer and strand dune associes are represented on the shore-line whilst the elevated central area shows the initiation of cactus-thorn scrub. Two areas, one in the north and one in the south, support Rhizophora and Avicennia. They were originally lagoons, they later became salt ponds and now are drying up with the result that Rhizophora is disappearing. There are also some plants, scattered and few in number, which are representative of strand woodland. The accompanying list shows the species found on this cay arranged according to the communities they represent.

Strand Pioneer and Strand Dune.
- *Calonyction tuba*
- *Euphorbia buxifolia*
- *E. blodgettii*
- *Heliotropium curassavicum*
- *Boerhavia scandens*
- *Cakile lanceolata*
- *Philoxerus vermicularis*
- *Sesuvium portulacastrum*
- *Canavalia obtusifolia*
- *Sporobolus virginicus*
- *Scaevola plumerii*
- *Caesalpinia bonducella*
- *Tribulus cistoides*

Cactus-thorn Scrub:
- *Pithecellobium unguis cati*
- *Acacia tortuosa*
- *Capparis ferruginea*
- *C. cynophallophora*
- *Morinda royoc*
- *Opuntia tuna*

Strand Woodland:
- *Cordia sebestana*
- *Coccoloba uvifera*
- *Thespesia populnea*
- *Cassia emarginata*
- *Piscidia piscipula*
- *Morinda citrifolia*

Mangrove Woodland:
- *Rhizophora mangle*
- *Avicennia nitida*
- *Laguncularia racemosa*
- *Conocarpus erecta*
- *Batis maritima*

Also found were:
- *Indigofera tinctoria*
- *Passiflora suberosa*

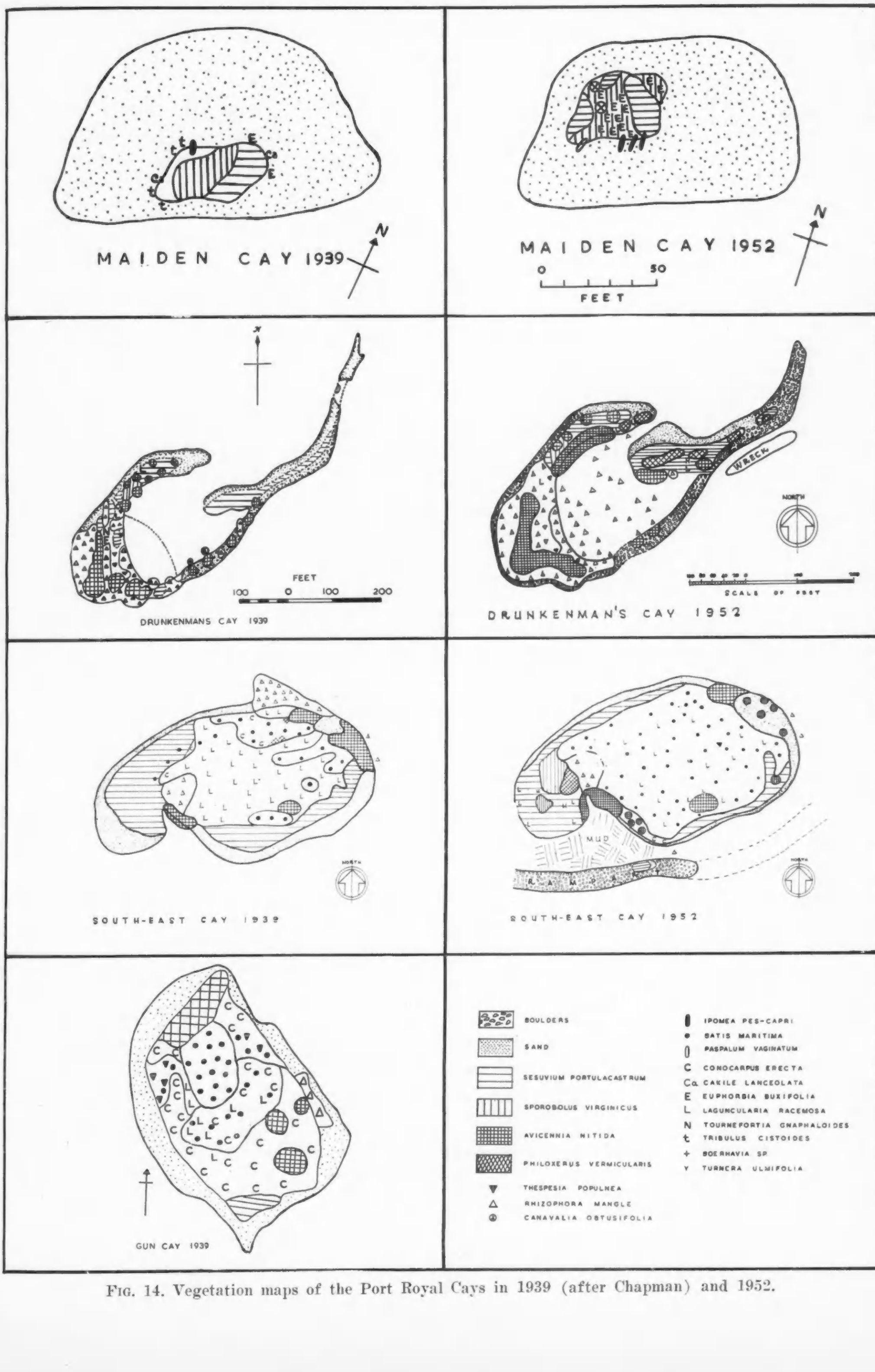


FIG. 14. Vegetation maps of the Port Royal Cays in 1939 (after Chapman) and 1952.

Maiden Cay

Maiden Cay is the smallest of the group and occupies an area of approximately 2,000 sq. yd. It consists entirely of sand, mostly under tidal influence, so that only about 200 sq. yd. is available for colonization. The highest point is only 4 ft. above the high tide mark. Fig. 14 shows that, from the period 1939 to 1952, there has been some slight change in the shore outline of the Cay due to sand movement but that the area occupied by vegetation has remained substantially the same. Only the pioneer and dune associates are represented and the latter is more in evidence at the moment indicating recent erosion. Since 1939, Sesuvium and Sporobolus have increased slightly in area whilst Euphorbia has spread into the Sporobolus zone. Two plants of Canavalia and one of *Paspalum vaginatum* have appeared and there are 4 specimens of Ipomea, none of which is flourishing extensively. Tribulus and Cakile, found in 1939, were not seen in 1952.

The contrast with the neighbouring Lime Cay is marked, Only 6 species of plants are to be found. Nevertheless, this small island, little more than a sand shoal, has remained more or less static for 13 years, during which time it has withstood the force of the major hurricane of 1951.

Gun Cay

Gun Cay was not visited by the authors but Chapman's vegetation map is reproduced (Fig. 14). Having an estimated area of 2,500 sq. yd., it is almost completely colonized so that the vegetation covers over ten times the area of that on Maiden Cay. The sand communities are represented only by Sesuvium and Sporobolus but all the mangroves are present as well as Batis and Thespesia. Chapman states that Tribulus was also recorded but he does not show it on his map.

Strand Pioneer and Strand Dune:

Sesuvium portulacastrum
Sporobolus virginicus
Tribulus cistoides

Strand Woodland:

Thespesia populnea

Mangrove Woodland:

Avicennia nitida
Laguncularia racemosa
Batis maritima
Rhizophora mangle

Drunkenmans Cay

Drunkenmans Cay, having 9,000 sq. yd. of land area, is characterized by having an outer "J" shaped rim of rock fragments in the shelter of which a lagoon has developed. The diagrams (Fig. 14) show that, since 1939, there has been considerable sand accumulation at the sea entrance to the lagoon. This may have been assisted by the protection afforded by a wreck which beached close to the windward east shore in 1948. Consequently, the main changes are an increase in the area covered by the sand communities and some encroachment of Rhizophora in the lagoon. Representatives of the maritime communities are shown below:

Strand Pioneer and Strand Dune:

Sporobolus virginicus
Sesuvium portulacastrum
Heliotropium curassavicum
Philoxerus vermicularis

Strand Woodland:

Thespesia populnea

Mangrove Woodland:

Rhizophora mangle
Avicennia nitida
Laguncularia racemosa
Conocarpus erecta

Chapman also records one plant each of *Tournefortia gnaphalodes* and *Euphorbia buxifolia.*

South East Cay

South East Cay has an area of 6,000 sq. yd. and has been built up in the shelter of an extensive rampart of rock fragments over 6 ft. high. It has undergone one minor change since 1939. The north shore has lost most of the Rhizophora and Avicennia and a small piece of coast due to storm action. There is also evidence that Avicennia is spreading on the muddy south shore where considerable protection is afforded by the rampart. Batis, too, has spread in the rocky centre of the island occupied by Laguncularia. *Sesuvium portulacastrum* now occupies a small patch of sand on the rampart. The communities present and their representatives are:

Strand Pioneer and Strand Dune:

Sesuvium portulacastrum
Sporobolus virginicus
Philoxerus vermicularis
Heliotropium curassavicum

Strand Woodland:

Thespesia populnea (one plant).

Mangrove Woodland:

Rhizophora mangle
Avicennia nitida
Laguncularia racemosa
Conocarpus erecta
Batis maritima

Morant Cays

The Morant Cays were not visited by the authors but Chapman has a vegetation map of Middle Cay, which has an area of over 14,000 sq. yd. This Cay may be taken as typical of those which are characterized by having a preponderance of Sesuvium and an absence of Batis and mangroves. The mere presence of such species as Boerhavia, Tournefortia and Turnera, occasional members of the tension belt between the dune and scrub associes on the mainland, is noteworthy although they are sparsely distributed.

Strand Pioneer and Strand Dune:

Cakile lanceolata
Ipomea pes-capri
Sesuvium portulacastrum
Portulacca oleracea

Philoxerus vermicularis
Sporobolus virginicus
Turnera ulmifolia
Boerhavia scandens

Strand Scrub:
Tournefortia gnaphalodes (one plant).

The cays are very reminiscent of the sand spits, both as regards their vegetation and methods of topographic development. Thus, sand cays such as Maiden Cay and Lime Cay in which the area, elevation and degree of protection depend entirely on sand accumulation, find their counterpart in sandy spits such as the Hellshire Spit. Rocky cays such as Drunkenmans Cay and South East Cay are similar to the Palisadoes where, in the early stages of development, considerable protection is afforded by the piling up of rock fragments. The suggestion that the Palisadoes has been formed by a fusion of isolated cays may appear to be a reasonable one but the possibility of its development by sand accumulation on the lee side of an extensive rampart should be borne in mind. In both types of cay, of course, sand accumulation is a major factor in the development of both topography and vegetation.

The zonation of plant communities also follows the same general pattern on both the cays and the spits. On the small Maiden Cay, as on the narrow and youngest part of the spits, only the Strand Pioneer and Strand Dune associes are represented. Increase in area and elevation, as on Lime Cay and the wider parts of the spit, leads to the appearance of cactus-thorn scrub and members of the Coccoloba-Thespesia association. Moreover, at any stage where there is sufficient protection (which may be relatively late on the sand cays and early on the rocky cays), mangrove woodland is to be found.

Facts concerning the vegetation of the cays in relation to area and distance from the mainland have been assembled in Table 5. There appears to be direct relationship between number of species and size in the case of the Port Royal Cays. Lime Cay, the largest, yields the greatest number of species (33) representing 5 different communities and it is the only one in which the cactus-thorn scrub is represented. At the other extreme, Maiden Cay only supports 6 species representing two communities. The other members of the Port Royal group are intermediate in size and number of communities present. It would be unwise, however, to conclude that size is the only factor. It has already been pointed out that mangroves will appear at any time providing there is sufficient protection. Such protection is not governed by area but by topography so that the configuration of the land necessary to provide sufficient shelter may be present very early in the life of the rocky cays even when they are small; in the case of the sand cays, this must await increase in elevation by sand accretion which is related to area. Such considerations might equally well be applied to the development of strand woodland. Furthermore, the area-vegetation concept again breaks down in the case of the Morant Cays. Middle Cay is next in size to

TABLE 5. The plant communities on the cays in relation to area and distance from mainland.

Cay	Distance from main-land in miles	Area in sq. yds.	Communities Represented: Pioneer	Dune	Strand wood-land	Mangrove	Cactus-thorn scrub	Total	Total number of spp.
Lime	1.2	30,000	X	X	X	X	X	5	33
Drunkenmans	1.8	9,000	X	X	X	X	–	4	11
South East	2.8	6,000	X	X	X	X	–	4	10
Gun	0.25	2,000	X	X	X	X	–	4	9
Maiden	1.8	200	X	X	–	–	–	2	6
Middle	30.0	14,000	X	X	–	–	–	2	10
Pedro	60.0	......	X	X	–	–	–	2	5

Lime Cay and would appear to be of the same type, yet only ten species are present. These represent three communities, and mangroves are not included. It may well be that distance from the mainland is a factor here, a hypothesis receiving further support when it is noted that, according to Lewis (1947), the Pedro Cays, 60 mi. from the mainland, have only five species of land plants, *Sesuvium portulacastrum, Portulaca oleracea, Cyperus brunneus, Tournefortia gnaphaloides* and *Suriana maritima*. In conclusion, therefore, the major factors to be co-related when considering the vegetation of the cays, are area, degree of protection and distance from the mainland.

THE LOWLAND COMMUNITIES

LIMESTONE

Two distinct vegetational units on limestone rock are recognized in this paper, i.e. dry limestone scrub forest and wet limestone forest.

Some two-thirds of the island is a limestone plateau and this is composed of hard limestone rock and derived soils which are about equal in area. The soil is predominantly of the bauxitic "terra rossa." Most of this is under cultivation and is dealt with separately.

On the rocky areas, rainfall is the controlling factor. The coastal limestone ranges of the south are arid to an extreme, weathering is slow and humus and organic matter almost absent. The area is greatly influenced by the seasonal rainfall and has more than six months when rainfall is under 4 in. Inland, the rainfall is high (75-100 in.) and, although the drainage is extremely rapid, the drought factor is moderate (See Fig. 6).

Aspect is related to wind exposure, humidity and drainage, but altitudinal changes, limited to about 3,000 ft., have little effect on the climax vegetation although they may influence secondary growth types.

Geologically, there are six different types of limestone in Jamaica ranging from cretaceous to recent coralline types. By far the most common is the white limestone of the Upper Eocene and Lower Miocene. This is hard and massive and, under certain climatic conditions, gives a characteristic clinker honeycomb rock common to the arid coastal hills and much of the karst area of the Cockpits. The most important

distinction for ecology is, however, between hard and soft (chalky) limestones which give rise to different soils.

Swabey (1942) considered the "limestone formations" as edaphic climaxes. Dry limestone scrub forest is developed where the rainfall is not more than 40 in. per year, with some months having below 2 in. rainfall. It is particularly evident on the south coast and includes an arid coastal fasciation. Wet limestone forest with its moist fasciation is typical of the more elevated inland areas such as the Cockpit country and Mt. Diablo plateau. In the dry regions, the rock is almost bare, such soil as exists being confined to the pockets and fissures of the rock. In the wet regions, erosion has proceeded more rapidly to give small hollow basins (Cockpits) in which bauxite soil has accumulated to a depth of from 5-50 ft. The wet limestone areas, then, necessarily have two aspects—the rocky slopes of the rim surrounding the cockpit and floor of the basin. Many of the latter are now under cultivation.

DRY LIMESTONE SCRUB FOREST AND THE ARID COASTAL FACIATION

Along the southern coast of Jamaica there is a series of rocky limestone hills and ranges, for the most part under 2,000 ft. elevation. These areas have a rainfall of less than 40 in. during the year, distributed in two rainy seasons. There is a drought period of more than six months. The north coast has few such areas, an example being the north coast of Trelawny (Fig. 6). Never very far from the sea and often extending through to the coast, these arid hills are of fissured, honey-comb, white limestone. They support a xeric scrub-forest of particular interest to the ecologist.

The main limestone areas of the south coast from east to west are found at Morant Bay, Yallahs, Dallas and Long Mountain, and, west of Kingston harbour, at the Hellshire Hills and Portland Ridge. Further inland and running at right angles to the coast, are the Don Figuerero and Santa Cruz Mts., in St. Elizabeth Parish. Around Negril at the extreme western part of the island, is an elevated coral shelf. The dry limestone hills of Trelawny on the north coast are low-lying and some three miles from the sea. Where the limestone reaches the sea, there is a narrow zonal aspect which is here considered as an arid coastal faciation.

DRY LIMESTONE SCRUB FOREST

Dry limestone scrub forest is a sparse, vegetational cover of low forest and tall scrub growing on bare limestone rock. No soil is present except for that deposited in small crevices or washed down to level areas. Leaf litter is almost nil and the floor is either a jumble of broken stone or a more or less continuous mass of jagged honeycomb rock.

The plants find support and sustenance by developing long, branched root systems which sprawl over and around the rocks to enter every crevice and canny. Species make-up may change rapidly from station to station, depending on aspect, slope and drainage as well as on soil deposits.

Red birch (*Bursera simaruba*) is ubiquitous as a scattered emergent tree, prominent for its copper red, flaky bark and complete deciduousness in the dry season. It has been suggested that its prevalence is due to fire resistance and selective cutting as the wood is regarded as useless for lumber.

In sheltered ravines, the tall cotton tree (*Ceiba pentandra*) may invade from the dry coastal plains and savanna. *Tecoma stans*, also deciduous, appears out of place here with its soft green pinnate leaves and yellow trumpet flowers. A host of small xerophytic trees and shrubs make up the mass of the vegetation. On a typical ridge such as Long Mountain, three narrow altitudinal zones may be correlated with soil accumulation and drainage. There is a lower zone where species from the adjoining alluvial plains form a tension belt on the bauxitic soil. These include Acacia, Haematoxylon, Guaiacum, Tamarindus, Albizzia, Piscidia, Leucaena and Guazuma.

A middle belt is dominated by low shrubs (Croton, Tecoma, Lantana, Morinda, Eugenia, Vernonia). The summit is often a thicket of Rhus, Dipholis, Gymnanthes, Hypelate and others. Larger trees are found in the moist ravines and may include a few of the trees from the moist inland limestone (Brosimum, Nectandra).

There is no distinct stratification, and structure varies from low scrub to a thin forest with trees 40 ft. and over. The canopy is always thin, even when continuous. Many of the species are semi-deciduous during the dry season. The trees are thin-boled, spindly and branch low to the ground.

Climbing and scrambling plants are well represented, although true lianes are absent. Epiphytes are restricted to xerophytic bromeliads, orchids and cacti. While some of the plants are thorny (Randia), this is not characteristic. Leaf size and texture is prominantly microphyllous and coriaceous. Many of the plants (*Croton linearis*) show a prolonged daily wilting at the height of the dry season. Compound leaves are seen in Bursera, Rhus, Piscidia, Tecoma, Hypelate, Simaruba, Spathelia, Amyris, Comocladia, and Picramnia.

A ground layer is frequently absent and, when present, is made up of a few ferns, *Peperomia* sp., cacti or woody perennial herbs. Xerophytic pasture weeds readily colonize open areas where depth of soil is sufficient.

Small palms and agaves give character when present.

Floristic Composition—Trees (from 15-40 ft. according to station) arranged in approximate order of frequency are:

Bursera simaruba
Tecoma stans
T. leucoxylon
Hypelate trifoliata
Bauhinia divaricata
Rhus metopium
Amyris balsamifera
A. elemifera
Gymnanthes lucida
Dipholis salicifolia

Spathelia sorbifolia
Clusia rosea
Capparis ferruginea
Gymnanthes elliptica
Comocladia pinnatifolia
Picramnia antidesma
Simarauba glauca
Capparis cynophallophora
Diospyros tetrasperma
Krugiodendron ferreum
Guettarda argentea
Sarcomphalus laurinus
Piper amalago
Sabel jamaicensis, the broadthatch palm, may be locally dominant.

Under Shrubs

Small shrubs of 10 ft. and more: (Order given approximates to frequency except that all members of a genus are grouped together).

Eugenia axillaris
E. monticola
E. rhombea
Allophyllus pachyphyllus
A. jamaicensis
A. cominia
Psidium albescens
Brya ebenus
Capparis flexuosa
Pisonia aculeata
Tournefortia hirsutissima
T. astrotrichia
Guettarda elliptica
Canella winterana
Morinda royoc
Portlandia grandiflora
P. latifolia
Erythroxylon rotundifolium
Bernardia caprinifolia
Adelia ricinella
Senecio discolor
Casearia hirsuta
C. nitida
Cestrum diurnum
Ayenia laevigata
Phyllanthus angustifolius
Bocconia frutescens
Psychotria balbisiana
Eupatorium dalea
Rondeletia trifolia
R. hirta
Caesalpinia sepiaria (naturalized)
Daphanopsis occidentalis

Small bushes up to 5 ft. or more include:

Croton linearis
C humilis
C. glabellus
C. flavens
C. grisebachianus
Lantana crocea
L. involucrata
Randia acuealata
R. jamaicensis
Malpighia glabra
M. punicifolia
Schaefferia frutescens
Abutilon giganteum
Vernonia divaricata
Rondeletia tomentosa
Melochia tomentosa
Castela macrophylla
Acalypha scabrosa
Helicteres jamaicensis
Argythamnia candicans

Climbers:

Abrus precatorius
Stigmaphyllon emarginatum
Cissampelos pareira
Clematis dioica
Smilax balbisiana
Passiflora perfoliata
P. rubra
P. suberosa
Paulinia barbardense
Serjania laevigata
Chiococca alba
Echites suberecta
E. umbellata
Thunbergia fragrans
Cucumis anguria
Ipomea quinquefolia
I. umbellata
I. sidaefolia
I. jamaicensis
Cardiospermum grandiflorum
Gouania lupuloides
Centrosema virginianum
Mucuna pruriens
Galactia pendula
Bidens reptans
Durantia plumieri
Lasciacis divaricata (scrambling bamboo grass)
Aristolochia odoratissima
Metastelma sp.
Mikania sp.

Epiphytes:

Tillandsia recurvata
Broughtonia sanguinea
Cereus flagelliformis

Parasites:

Phorandendron spp.

Herbs:

Stachytarpheta indica
Corchorus siliquosus
Heliotropium parviflorum
Asclepias curassavica
Andrographis paniculata
Blechum brownei
Tournefortia volubilis
Cordia globosa
C. cylindrostachya
Erigeron canadensis
Eupatorium odoratum
Sonchus oleraceus
Verbesina pinnatifida
Vernonia divaricata
Amaranthus viridis
A. spinosus
Euphorbia hirta
Tragia volubilis
Priva echinata
Spigelia anthelmia
Sida procumbens
S. rhombifolia
Argemene mexicana

Rivina humilis
Crotalaria retusa
C. verrucosa
Desmodium supinum
Waltheria americana
Turnera ulmifolia
Croton ovalifolius
Salvia occidentalis
Hyptis capitata

The ferns *Pteris longifolia, Adiantum melanoleucum, A. tenerum, Cheilanthes microphylla* are widespread but not abundant.

The above type of forest which is typical of the dry coastal hills at the present time, has been subject to much human interference by periodic burning. The larger trees have been removed for timber and firewood so that little remains of former canopy and sub-canopy trees. Fortunately, there is still one relatively undisturbed area at Portland Ridge on the south coast. Some of the more valuable timber trees here have been removed but, nevertheless, sufficient remain to give a good representation of the type of forest that formerly existed in the dry limestone regions. The identity of many of the trees from this area forms the subject of a valuable report by Lewis (1947) who recognized over 80 species. Since the lower layers of the forest are essentially similar in structure and species to that already described, although less well-developed in this denser woodland, remarks are confined to the tree layers. The canopy is open and varies in height according to station from 40-60 ft. with sporadic emergents up to 80 ft. or more. The sub-canopy is more closed, reaches a height of 20-35 ft. and may include the palms *Coccothrinax fragrans* and *Thrinax parviflora* (Fig. 15). The maximum development is reached in the flatter areas of the ridge where leaf litter and humus cover the limestone. Only four species are completely deciduous. *Swietenia mahogoni, Bursera simaruba, Spondias monbin* and *Plumiera* sp. However, many of the species classed as evergreen lose some of their leaves during the prolonged dry season.

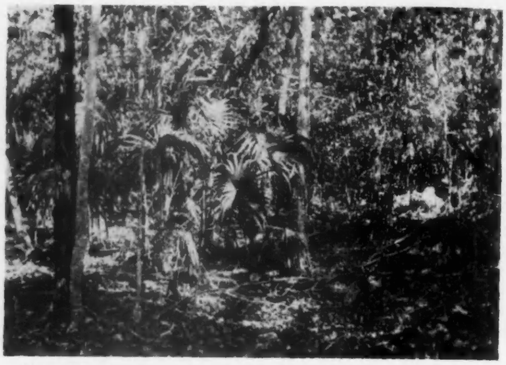


Fig. 15. An open aspect of Dry Limestone Forest at Portland Ridge. The palm is *Thrinax parviflora.*

Floristic Composition

Occasionally emergent (70-80 ft.)

Chlorophora tinctoria
Pisonia fragrans
Rhamnidium jamaicense
Sapota sideroxylon
Swietenia mahogoni
Tecoma leucoxylon

Canopy (40-60 ft.)

Adelia ricinella
Allophyllus jamaicensis
Amyris elemifera
Brosimum alicastrum
Bumelia retusa
Bursera simaruba
B. simplicifolia
Caesalpinia vesicaria
Calyptranthes chytraculia
C. pallens
C. zuzygium
Citharexylum fruticosum
Colubrina reclinata
Cordia gerascanthoides
C. nitida.
Diospyros tetrasperma
Erythroxylon areolatum
Eugenia axillaris
Exothea paniculata
Exostema caribaeum
Guazuma ulmifolia
Hippomane mancinella
Krugiodendron ferreum
Matayba apetala
Melicocca bijuba
Picrodendron baccatum
Pisonia obtusata
Rhus metopium
Sideroxylon foetidissimum
Tamarindus indica

Sub-Canopy (20-30 ft.)

Albizzia berteriana
Anona squamosa
Bauhinia divaricata
Bourreria succulenta
Bumelia rotundifolia
Brya ebenus
Canella winterana
Capparis cynophallophora
C. ferruginea
C. flexuosa
Casearia quianensis
Cassia emarginata
Cereus peruvianus
Clusia flava
Coccoloba spp.
Coccoloba krugii
Coccothrinax fragrans
Comocladia velutina
Cordia sebestana
Crescentia cujete
Croton glabellus
Erythroxylon rotundifolium
Eugenia monticola
Guaicum officinale
Gymnanthes lucida
Haematoxylon campechianum
Hypelate trifoliata
Linociera ligustrina
Ocotea jamaicensis

Oxandra lanceolata
Peltophorum brasiliense
Phyllanthus acuminata
Piscidia piscipula
Plumeria sp.
Sarcomphalus laurinus
Thrinax parviflora
Ximenia americana
Zanthoxylum fagara
Z. spinosum

It will be evident then that the forest here has a very rich flora. It provides an important remnant that would well repay detailed study.

ARID COASTAL FACIATION OF DRY LIMESTONE SCRUB FOREST

The environment of the arid coastal regions of the Caribbean has been graphically described by Seifriz (1943): "The heat is intense, the light blinding, every plant armed, no water, no shade, no trail leading anywhere, as awe-inspiring, as fearful, as superb a picture of the eternal persistence of life under the most adverse conditions that nature can produce."

Perhaps the most notable aspect is the mass of bare, jagged, honey-comb limestone over which one must clamber. The coastal limestone has weathered into a sharp clinker-like, honey-comb rock which has a metallic ring to hob-nailed boots. Sharp-pointed and knife-like edges surround the many small crevices and pockets where the sparse soil and organic debris may accumulate. Every crack and fissure is utilized for the tenacious, if precarious, root-hold of tree and shrub, many of which appear to be growing out of solid rock.

For a distance of over 50 mi. along the south coast from Morant Bay to Portland Point, there is an almost unbroken rim of low limestone hills where this aspect of the limestone vegetation is well developed. The area is arid to an extreme, total rainfall is below 30 in. and there are 6 to 10 months having less than 4 in. with some under 1 in.

The xerophytic vegetation is tolerant of salt spray and sweeping winds. The air has a high evaporating power. It is a littoral woodland on coastal limestone made up of hard-leaved, dry limestone shrubs together with cacti, halophytes and salt-resistant trees not encountered inland. The flora is relatively rich for such an area and merges imperceptibly into typical dry limestone scrub-forest species.

A feature of the faciation is the presence of cacti of which the dildo (Cereus), forming columns up to 20 ft. high, is abundant. Such cacti occur only here and in the thorn-scrub in Jamaica.

In sheltered bays, the littoral fringe of the limestone may be occupied by Rhizophora although Chapman regarded this as an unstable community. Where mud has been deposited, other mangroves may be present in front of the limestone rock. Small bays in the limestone coast are frequently enclosed by spit formation, first forming a lagoon then a saline flat with typical halophyte communities. In the same way, sand deposited to seaward gives typical strand trees (Coccoloba, Thespesia) within limestone areas. Again, where alluvial plains reach the coast, Prosopis and Acacia may invade soil pockets on the limestone.

Of the limestone scrub-forest itself, typical coastal trees are:

Hippomane mancinella
Cordia sebestana
Plumiera alba
Piscidia piscipula
Comocladia velutina
Chrysobalanus icaco
Parkinsonia aculeata (naturalized).
Jacquinia armillaris
Citharexylum fruticosum
Capparis ferruginea
Caesalpinia vesicaria
Pithecellobium unguis-cati

Other common trees and shrubs in approximate order of frequency are:

Rhus metopium
Bauhinia divaricata
Hypelate trifoliata
Bursera simaruba
Pisonia obtusata
P. fragrans
Gymnanthes lucida
Eugenia monticola
Amyris elemifera
Matayba apetala
Calyptranthes chytraculia
C. pallens
Capparis flexuosa
C. cynophallophora
Krugiodendron ferreum
Peltophorum braziliense
Clusia flava
Canella winterana
Sapota sideroxylon
Guaiacum officinale
Oxandra lanceolata
O. laurifolia
Beureria succulenta
Cordia gerascanthoides
C. nitida
Bursera simplicifolia
Coccoloba spp.
Tecoma leucoxylon
Ficus populnea

Occasional trees and shrubs:

Exostema caribaeum
Erythroxylon aveolatum
E. rotundifolioum
Melochia tomentosa
Laetia thamnia
Diospyros tetrasperma
Eugenia axillaris
Sarcomphalus laurinus
Zanthoxylum fagara
Z. flavum
Exothea paniculata
Meliococca bijuga
Bumelia retusa
B. rotundifolia
Lasiocroton macrophyllus
Securinega acidoton
Picrodendron baccatum
Adelia ricinella
Phyllanthus acuminatus

P. linearis
Sideroxylon foetidissima
Gymnidia latifolia
Casearia guianensis
Swietenia mahogoni
Catesbaea parviflora
Agava americana
Croton linearis

Palms:

Coccothrinax fragrans
Thrinax excelsa
T. parviflora

Herbs:

Heliotropium curassavicum
Melochia tomentosa
Schaefferia frutescens
Ambrosia hispida
Helicteres jamaicensis
Jatropha gossypifolia

Climbers:

Chiococca alba
Cissampelos pareira
Cissus cucurbitacea
Metastelma harrisii

Cacti:

Cereus peruvianus
Opuntia tuna
O. jamaicensis
O. spinosoissima
Melocactus communis

WET LIMESTONE FOREST

This community is developed in areas of limestone rock where the rainfall is over 75 in. and may range up to 150 in. For the most part, it is at elevations from 1,000 ft.-2,500 ft. and situated inland. No doubt, there are different fasciations within this type which will be recognized with further study.

The largest area of wet limestone forest is in the Cockpit country, although the type is found on certain of the limestone peaks (Mt. Diablo and Dolphin Head) along the central axis of the island. It is also present on some coastal ridges of the wet northwest coast.

Mt. Diablo, 3,300 ft. is a precipitous, calcareous plateau, very similar to the Cockpit area further west. Dolphin Head (1,780 ft.) is a limestone peak in the centre of calcareous shales.

The John Crow Mountains of limestone in the extreme eastern end of Jamaica do not fall into this unit. Due to the very high rainfall of some 300 in. per year, and their height of almost 4,000 ft., they are clothed with lower montane rain forest on the lower slopes and an elfin woodland on the summit.

The Cockpit country is so-called because the whole area is made up of circular depressions (dolinas) up to 500 ft. deep filled by bauxitic soils with accumulated humus from the surrounding rim of limestone rock. The area is typical karst country where underground drainage, subterranean rivers, sinkholes and caves are common. Many of the depressions are the result of sinkholes from underground streams.

The reduction of the Cockpit plateau has not yet proceeded to the level seen in comparable areas in Cuba and Porto Rico where the "mogotes" or haystack hills represent blocks of rock partly weathered down and having their bases engulfed by the rising plain of soil about them. With time, many of the smaller valleys and depressions in the Cockpit country will join up until only the highest hills will be left.

Burning and cultivation have affected many areas, both in the valleys and on slopes with the production of "ruinate"; however, much still remains relatively undisturbed.

The forest is of two types—that on the bare limestone rock and that on the valley floor. The soil of the latter, which may be anything from 5 to 50 ft. in depth, is bauxitic and has very free drainage, a neutral to alkaline pH and a general deficiency in phosphates. There is, of course, much overlapping of species between the two types of forest and it is mainly the general physiognomy that is different on rock and soil (Fig. 16). As previously mentioned, most of the valleys have been cleared and planted with bananas and other crops such as sugar, yams, coco (Colocasia) and cassava. Fig. 17 shows a clearing in the forest that has been planted with Colocasia and Yams.

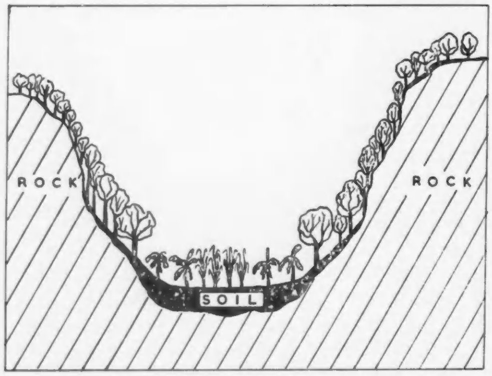


Fig. 16. Diagrammatic profile of typical Cockpit country supporting Wet Limestone Forest. Different aspects can be related to depth of soil which is greatest in the valley bottom and grades to bare rock on the slopes. The larger valleys are now under cultivation or pasture.

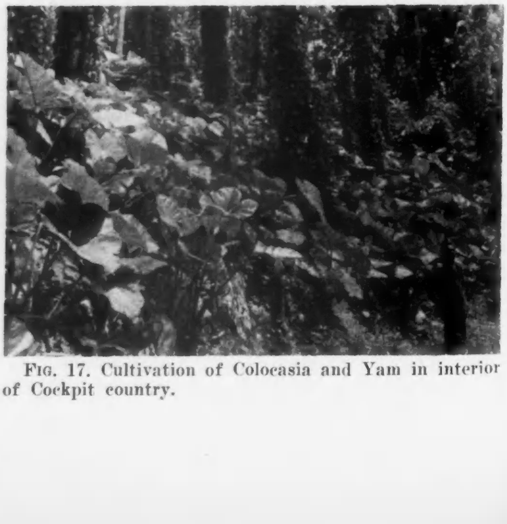


Fig. 17. Cultivation of Colocasia and Yam in interior of Cockpit country.

The wet limestone forest (Fig. 18) is far more mesophytic and luxuriant than the dry type, having more forest trees, epiphytes and lianes, aroids, bromeliads and orchids. Undergrowth is often sparse due either to the rocky substratum or the dense shade. However, there are more open aspects where *Aechmea paniculigera*, *Polypodium* spp., and aroids are prevalent (Fig. 19).

FIG. 18. View of Wet Limestone Forest looking down into one of the cockpits.

FIG. 19. An open aspect of Wet Limestone Forest showing climbing aroids, *Aechmea paniculigera* (bottom right) and *Polypodium crassifolium* (bottom left).

STRUCTURE

The canopy of the forest is more or less uniform at 50-60 ft., except that in the Cockpits *Terminalia latifolia* and *Cedrela odorata* are emergent trees, 80-100 ft. high. The canopy, although typically closed, is never dense and is made up of tall thin-boled trees 1-2 ft. in girth and branching at 40 ft., into a wide spreading crown with little depth.

A sub-storey of small trees averaging 40 ft. in height may be distinguished. This is often quite dense and made up of its own characteristic species.

The shrub and field layers are sparser than the strata above and often merge together. In fact, undergrowth is generally lacking due to the rocky substratum. Small buttresses may be seen but are not a feature. Clusia and Lucuma develop stilt roots. The larger trees show scattered distribution but frequently the forest is composed of closely spaced, small trees and shrubs of similar life form, forming a type of tall thicket.

Much local variation occurs due to sharp changes in aspect and drainage. The vegetation of valleys is consistent but the slopes may reflect wet and dry aspects by the presence and luxuriance of the epiphytes and ground herbs, whilst tree species differ. Soil depth and leaf litter are noticeably less in the drier aspects. The profile diagram (Fig. 20) is of a typical moist slope forest.

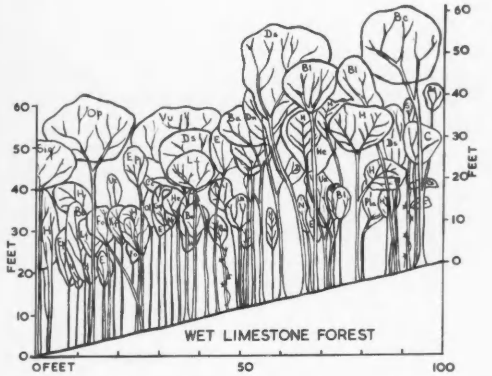


FIG. 20. Profile diagram of Wet Limestone Forest measured in the Cockpit country. The trees are included from a strip 100 ft. long and 25 ft. wide.

KEY TO SYMBOLS: Ai. *Andira inermis* (Wormwood); Ba *Brosimum alicastrum* (Breadnut); Bb *Bucida buceras* (Olive bark tree); Bc. *Buchenaria capitata* (Mountain wild olive); Bl. (Bloodwood); C. *Coccoloba* sp. (Grape); Cc. *Cinnamodendron corticosum* (Mountain cinnamon); Cs. *Comocladia* sp. (Maiden Plum); D. *Dipholis* sp. (Bulletwood); Dn. *Dipholis nigra* (Galimenta, Red Bullet); Ds. *Dipholis salicifolia* (Black bullet); E. *Eugenia* sp. (Rodwood); Ep. *Exothea paniculata* (Wild Ginep); Fo. *Faramea occidentalis* (Wild Coffee); Gg. *Guarea glabra* (Alligator, Wild akee); H. *Drypetes lateriflora* (Whitewood, Guiana plum); Kf. *Krugiodendron ferreum* (Black ironwood); Lf. *Lasiocroton fawcettii*; N. *Nectandra* sp. (Sweetwood); Ol. *Oxandra lanceolata* (Black lancewood); Op. *Ochroma pyrimidale* (Balsamwood); Pla. *Plumeria alba* (Frangipani); Si. g. *Simaruba glauca* (Bitter damson); Sj. *Sapium jamaicense* (Blindeye); Vu. *Vitex umbrosa* (Fiddlewood, Boxwood); U.K. Unidentified.

Lianes are represented by climbers, some of which may also be classed as epiphytes. Climbing aroids are abundant throughout and everywhere their long, dry, thin roots hang down from the trees. Polypodium is a common climbing fern. Other climbers are: the prickly Smilax, Dioscorea, *Rajania cordata* (found only in the Cockpit area), and leguminous vines.

Of the bromeliads, species of *Tillandsia* are trunk epiphytes. Hohenbergia is a true perching epiphyte confined to the crowns of the larger trees at 40 ft. *Aechmea paniculigera* is common on the floor in rock crevices, together with ferns and mosses.

Small shrubs are represented by Piperaceae, Melastomaceae, Rubiaceae and the short-thatch palm *Thrinax tesselata*. Tree ferns are localized although many other ground ferns reach considerable size.

The trees are evergreen but some are semi-deciduous in other habitats. Leaves, for the most part, are

simple, but compound leaves occur in Pithecellobium, Simaruba, Mesquitoxylon, Picraena and Zanthoxylum.

FLORISTIC COMPOSITION

The true climax in the small deep valleys is a Terminalia-Cedrela association. Both of these however, are valuable timber trees and the fact that they are found growing in fertile valleys has led to intensive exploitation.

A floristic name cannot be so easily applied to the forests of the rocky limestone slopes surrounding these valleys.

Large trees which are common enough throughout are: *Terminalia latifolia, Cedrela odorata, Calophyllum jacquinii* and *Pithecellobium alexandri.*

Frequent dominants of the canopy layer are the breadnut (*Brosimum alicastrum*), the sweetwoods (*Nectandra* spp.), and the bulletwoods (*Dipholis* spp.).

A list of the trees in approximate order of frequency is:

Brosimum alicastrum
Nectandra antillana
N. sanguinea
Dipholis nigra
Pithecellobium arboreum
Zizyphus chloroxylon
Ficus sp.
Zanthoxylum martinicense
Sloanea jamaicensis
Buchenavia capitata
Lucuma mammosa
Mimusops excisa
Podocarpus purdieanus
Cecropia peltata
Prunus occidentalis
Psidium montanum

The sub-canopy layer of small trees reaches 40 ft. and contains many species, not all of which may be present in any one aspect. This stratum often merges into the canopy above and species may be common to both.

Trophis racemosa
Antirrhoea jamaicensis
Zanthoxylum flavum
Simaruba glauca
Spathelia glabrescens
Mosquitoxylon jamaicense
Picraena excelsa
Eugenia axillaris
Eugenia spp.
Colubrina ferruginosa
Matayba apetala
Prunus myrtifolia
Lagetta lagetto
Miscnteca triandra
Gucrea glabra
Exothea paniculata
Sapium jamaicense
Amyris balsamifera
Bauhinia divaricata
Rondeletia spp.
Hufelandia pendula
Ocotea staminea
Xylopia muricata
Oxandra lanceolata
Comocladia pinnatifolia
Andira inermis

The families Sapotaceae and Lauraceae are well represented in the above lists.

The shrub layer includes a few smaller trees and bushes such as *Piper nigrinodum,* many Melastomaceae, *Bocconia arborescens, Carica jamaicensis, Coccoloba longifolia, C. diversifolia, Acidoton urens* and *Clusia rosea.*

Climbers and epiphytes include the climbing shrub, *Rourea paucifoliata,* aroids, *Begonia glabra, Dioscorea polygonoides,* the wild yam, and abundant *Polypodium heterophyllum.*

Bromeliads are frequent, many species of *Hohenbergia* being present such as *H. distans, H eriostachya* etc.

The field layer has a few herbs such as *Gyrotaenia spicata, Peperomia amplexicaulis, P. cordifolia, Pilea ciliata, P. crassifolia* and *P. reticulata, Boehmeria jamaicensis* and, on the edges of clearings, *Pachystachys coccinea.*

Ferns are prominent and frequent members of this layer. The commonest dryopteroid is *Thelypteris serrulata.* Other characteristic species are *T. oligophylla, T. patens, T. venusta, T. sagittata, Ctenitis ampla* and *C. effusa.*

On limestone ledges throughout is to be found *Thelypteris asterothrix* especially where the rocks overhang above. One can assume that this species thrives best where not exposed to direct wetting.

Other ferns of the wet limestone forest include *Lomariopsis underwoodii,* found sterile except where scandent on tree-trunks, *Campyloneurum augustifolium, Polystichum christianae, Polypodium dissimile, P. heterophyllum,* the filmy ferns *Trichomanes* spp. and the ferns of moist glades such as *Dennstaedtia bipinnata,* with fronds up to 10 ft. long, *D. cicutaria* and *Pteris quadriaurita.*

Mosses are sparse but include:

Thuidium involvens (Hedw.) Mitt.
Leucobryum antillarum Schp.
Entodon macropus (Hedw.) C. M.
Fissidens donnellii Aust.
Hookeriopsis fissidentoides (H. & W.) Jaeg.
Orthostichopsis tetragona (Hedw.) Broth. (pendant from trees).
Isopterygium tenerum (Sw.) Mitt. (on trunks).

Wet limestone forest also includes a moist fasciation seen in such areas as the Red Hills, west of Kingston. Rainfall is the controlling factor and there is a mingling of the dry and wet limestone forest species with some modification in structure. This fasciation has not been fully studied.

VEGETATION OF THE BAUXITE PLATEAUS

This cannot be regarded as an ecological formation but it is a convenient heading for the areas of extensively cultivated limestone soils of Jamaica. The original vegetation was forest which merged into the present limestone forest types.

It has been observed that Jamaica is comprised of some three-quarters limestone and its derived soils.

Much of the limestone is still seen as rocky hills and ranges but, in karst areas, there are frequent depressions and sinkholes in which soil has accumulated. The parishes of Manchester and St. Ann constitute upland plateaus with a covering of residual bauxitic soils, varying much in depth, over the parent limestone. Such bauxitic soils are known locally as "terra rossas" and are now being actively exploited for bauxite, the ore of aluminium.

"Terra rossa" soils vary according to development and there are many "degraded" types where impurities give impeded drainage, or fertility values are lowered. Phosphate deficiency is general. The soils of such large inland valleys as St. Thomas in the Vale are regarded as lacustrine deposits from ancient lakes. The soil here is heavy clay with poor drainage and is generally acid (pH 4-5).

Rainfall over the "terra rossa" areas is, with one notable exception, over 60 in. per annum and there are few months with less than 4 in. The exception (Fig. 6) is along the north coast of Trelawny where the total annual rainfall is below 40 in. and there are at least six "drought" months with less than 4 in. "Terra rossa" here forms a narrow coastal strip under sugar cane or cattle pasture in which the tree members are essentially those migrating from the low, inland limestone ridges. *Swietenia mahogoni* and *Peltophorum braziliense* are abundant, together with *Cordia gerascanthoides, Guazuma ulmifolia, Zanthoxylum flavum, Bauhinia divaricata, Esenbeckia pentaphylla, Pimenta officinalis, Bursera simaruba, Dipholis salicifolia* and *Haematoxylum campechianum.*

The plateaus of St. Ann and Manchester have a higher rainfall and are areas of intensive agriculture and grazing. The induced savannas of the cattle pens have many of the larger forest trees from the surrounding wet limestone forests (Fig. 21).

Magnificent specimens of the cotton tree (*Ceiba pentandra*) and the West Indian Cedar (*Cedrela odorata*) are seen. Common, too, are large fig and guango trees (*Samanea saman* syn *Enterolobium saman*). These old trees are laden with epiphytes, climbers, stranglers such as *Solandra grandiflora* with its showy, pale yellow, trumpet blooms, *Schlegelia parasitica,* figs and Clusias, bromeliads, orchids, ferns and aroids.

FIG. 21. Remnant limestone forest and pasture on the Manchester plateau.

Smaller trees which are also frequent as isolated specimens are:

Guazuma ulmifolia
Terminalia latifolia
Pithecellobium arboreum
Cecropia peltata
Nectandra patens
Hibiscus elatus
Hura crepitans
Pimenta officinalis

Widespread shrubs include:

Pisonia aculeata
Psidium guajava
Morinda royoc
Solanum verbascifolium

Roadside and pasture weeds are:

Lantana involucrata
Sida spp.
Bidens pilosa
Borreria laevis
Asclepias curassavica
Mimosa pudica
Crotalaria retusa
Rivina humilis
Bryophyllum pinnatum
Eupatorium odoratum
Desmodium supinum
Stachytarpheta indica
Cordia globosa
Waltheria americana
Achyranthes indica
Tragia volubilis
Bromelia pinguin
Barleria prionitis
Anemia adiantifolia

Climbers:

Echites umbellata
E. suberecta
Stigmaphyllum emarginatum
Cissampelos pareira
Cissus sicyoides
Abrus precatorius
Clematis dioica
Momordica charantia
Tournefortia volubilis

In St. Ann, is found the largest area of rendzina soil developed over soft limestone. The hills are rolling, fertile, mainly under pasture and similar in aspect to the wetter shale regions.

While most of the "terra rossas" are free draining and neutral to alkaline depending upon the depth over the parent rock, the lacustrine basins are of greater age and the soil is termed "degraded terra rossa." Drainage is impeded, acidity high, whilst the texture is a heavy clay. These areas are extensively cultivated and grow breadfruit, citrus, mangoes, bananas, pineapples, coconuts, sugar and naseberry (*Achras sapota*).

Amongst the trees, many of the genera common to the plains and shale valleys are seen, such as:

Tamarindus, Chrysophyllum, Ceiba, Cecropia, Catalpa, Bauhinia, Samanea, Blighia, Poinciana, Terminalia, Erythrina, Spondias, Crescentia and *Pithecellobium alexandrii.*

The savannas of epiphyte-laden mango and guango trees, clumps of bamboo and Haematoxylon thickets show a distinct relation with the alluvial plains and lower shale hills, not shown by other communities. *Acacia* species are, however, altogether absent since they fall out rapidly once the alluvium is left.

ALLUVIUM

VEGETATION OF THE ALLUVIAL PLAINS

Large low-lying coastal plains are located along the dry southern coast. These have been formed as the broad alluvial deltas of meandering rivers. The rich alluvium of mixed sand, gravel and loam is spread out as a thick cover over the down-faulted limestone. On the coastline where ancient shallow bays were silted up, the alluvium is interbedded with layers of heavy marine clay. In the Ferry area, the history of such a plain can be easily visualised. The Rio Cobre has changed its course four times within colonial history, each time broadening out the plain. Alluvium is some 15 ft. in depth overlying 60 ft. of marine clay. In 1838, the river was diverted to a new mouth by a cut of some 7 mi. and, since that time, 200 acres of silt has been deposited at the mouth. Much of the saline area is at present being brought under cultivation from mangrove vegetation. Drainage first lowers the water table which kills the mangrove pneumatophores. Further flooding, drainage and cultivation prepares the land for para grass (*Panicum purpurascens*). Leaching continues and, within three years, sugar cane may be planted, being tolerant of salt in a concentration of 15 p.p.m.

The plains were fully exploited during the boom in sugar before the Napoleonic wars. With the decline in sugar after 1840, the cane areas decreased, large portions reverting to degraded, secondary types or turned over to cattle raising. For the most part, the alluvial plains are arable, fertile and suitable for irrigation, hence they are areas of high population and well-developed agriculture.

Starting from the east, are the small plains and river terraces of the Plantain Garden river in St. Thomas and the small deltas at the mouths of the Morant and Yallahs rivers.

Behind Kingston lies the dry Liguanea plain rising to 700 ft. a few miles inland and extending westward to join the Plains in Lower Clarendon parish. There are two inportant rivers here, the Rio Cobre and the Rio Minho. Much of the area is of irrigated cane fields. Nearer to the coast, there is a mosaic of highly saline and alkaline marine clays with Rio Minho alluvium and degraded "terra rossa" soils. The coastal areas are, therefore, unproductive and infertile (Croucher 1938).

The broad Manchester limestone plateau and limestone ranges separate the Clarendon Plains from the basin of the Black River which forms a low-lying flood plain reaching inland some 20 mi. along its course. The whole area of some 100 sq. mi. is an extensive sedge marsh, with the exception of the small dry Plains of Pedro skirting the Santa Cruz ranges.

In Westmoreland Parish, are the small George plains traversed by the Cabaritta river. They are low-lying and swampy.

On the north coast, the descent from the central mountains is more abrupt with shorter and swifter rivers. Alluvium is found as river terraces where the soil is more silty and free from saline influences.

The plains may vary from a few to 15 mi. in width and may be continuous for 20 mi. Generally they are hot, dry, low-lying and usually bounded by limestone hills although the Liguanea Plain merges into shale hills. Rainfall is often as low as 30-35 in., though most of the plains have from 40-60 in. Rainfall is uneven and the drought shadow of less than 4 in. of rain, for six or more months, falls over the coastal fringe. There is a coastal aspect marked from the inland aspect by soil, altitude and rainfall. Differences in soils, which may be the fertile free-draining alluvium, heavy saline and acid or alkaline clays with impeded drainage, degraded bauxitic soils or mixture of all, have profound influence upon the vegetation over small areas. Some of the marine clays have a salinity of 500 p.p.m. for the upper 6 in. and a pH of 5.2. At 2 ft. depth, the figures are 3,000 p.p.m. and a pH of 4.5. The plant communities are all induced, modified, secondary types and will be described under the following headings:

a) Cultivated areas and induced savanna.
b) Secondary communities.
c) Thorn scrub.

CULTIVATED AREAS AND INDUCED SAVANNA

In 1938, bananas provided over 50% of Jamaica's export trade and much of this banana land was on the plains. Coconuts are not extensive on alluvial soils. Important minor crops are tobacco, pineapples, tomatoes, maize, cashew nuts and, more recently, rice which will grow on irrigated marine clays.

The drier regions, where irrigation is so far impracticable, are given over to grazing without cultivation. Much is induced savanna of guinea grass (*Panicum maximum*) and the guango tree (*Samanea saman*) (Fig. 22). Guinea grass, now a common fodder grass, was unwittingly introduced from Africa with a consignment of birds in 1744. Other introduced grasses of the pastures are: *Andropogon pertusus, Cynodon dactylon, Sporobolus indica, Paspalum fimbriatum* and *P. saccharoides.*

Many of the characteristic trees of the southern plains were introduced in early colonial times and have become naturalised. It would be difficult to reconstruct the original vegetation but, no doubt, it was a sparse forest composed of such trees as *Guiacum officinale* ("lignum vitae"), a small tree with a bushy crown; *Catalpa longissima,* the handsome yokewood reaching up to 80 ft.; the deciduous cotton tree, *Ceiba pentandra,* of 120 ft.; *Hymenaea courbaril;* the gru gru palm, *Acrocomia aculeata*; and *Chlorophora tinctoria.* Smaller trees would have included

FIG. 22. Induced savanna of Guinea grass (*Panicum maximum*) and Guango trees (*Samanea saman*) on the alluvial plains.

FIG. 23. Thorn savanna, a second growth type, on the alluvial plains. The trees are *Acacia lutea, Pithecellobium dulce* and *Acacia farnesiana*. The grass is *Andropogon pertusus*.

Guazuma ulmifolia, Cordia gerascanthoides, Melicocca bijuga, Ficus mamillifera Enterolobium mangense, Crescentia cujete, Sapindus saponaria, Buchenavia capitata, Cassipourea elliptica, Trichilia hirta, Quiinia jamaicensis, Crataeva gynandra, Piscidia piscipula, and *Cordia alba*. The shrubs *Sarcomphalus laurinus, Erythroxylon areolatum, Brya ebenus, Anacardium occidentale* and *Cassia emarginata* would also have been present.

It is sometimes doubtful whether a tree is naturalized or native since there are more introductions here than anywhere else on the island. Samanea, with its sweet, mucilaginous pods relished by stock, was introduced with cattle from Central America. Together with the ubiquitous mango tree, it forms a characteristic part of the landscape. Both are laden down with epiphytic bromeliads and cacti.

Albizzia lebbeck, from the Far East, is the now familiar "woman's tongue" which reached Jamaica along with mango in 1782. The name refers to the chattering of the dry pods with the slightest breeze. Introduced *Cassia* species are common, together with such trees as: *Terminalia catappa, Adenanthera pavonina, Poinciana regia, Spathodia campanulata, Tamarindus indica, Casuarina equisetifolia, Moringa oleifera, Haematoxylon campechianum, Spondias monbin, S. purpurea, Zizyphus jujuba,* Coconut palms and several *Acacia* species.

Common roadside plants are: *Ricinus communis, Jatropha gossypifolia* and *Datura stramonium*. Also frequent are the twining, parasitic *Cuscuta americana* and polygonaceous *Antigon leptopus*.

SECONDARY COMMUNITIES

Ruinate is the delightfully apt term given to all marginal and abandoned lands in Jamaica. It is applied to the infinitely varied, secondary growth types of vegetation developing after burning, catch cropping and abandonment. On the alluvial plains, the common form that occurs is a thorn thicket or, under moderate cutting and grazing, a thorn-savanna. (Fig. 23).

The type of ruinate found indicates the previous history of the area, whether, for instance, it is abandoned arable or pasture land, or marginal land after catch cropping. The details of succession require further study.

Frequent pioneer weeds on denuded ground are: *Amaranthus spinosus, A. viridis, Cyperus rotundus, Heliotropium parviflorum, Portulacca oleracea, Cleome serrata, C. spinosa, Achyranthes indica, Pectis febrifuga, P. cillaris, Phyllanthus niruri* and other Euphorbiaceae. These species are common following the rains as ephemeral adventives emphasizing the fact that succession in the dry lowland tropics is complicated by seasonal factors.

The initial stages merge into a more stable community of secondary invaders, a few pioneers remaining to take their place in the final stages of the succession. Such secondary invaders include: *Cynodon dactylon* and *Andropogon pertusus* with herb weeds such as *Crotalaria retusa, C. verrucosa, Waltheria americana, Sida rhombifolia, Mimosa pudica* and other semi-woody perennials.

At this stage, shrub and tree seedlings of such plants as *Psidium guajava, Haematoxylon campechianum, Capsicum frutescens, Cestrum diurnum, Lantana crocea, Pisonia aculeata, Acacia lutea* and *Solanum verbascifolium* make their appearance.

Such ruinate may pass through to a thorn thicket or thorn savanna dominated by *Acacia lutea*, with common pasture weeds such as *Borreria laevis, Desmodium supinum, Sida* spp., *Boerhavia scandens, Euphorbia heterophylla, E. hypericifolia, Alternanthera repens, A. parvifolia, Celosia argentea, Amarantus* spp., *Leonurus sibiricus, Bidens pilosa, Gomphrena globosa, Plumbago scandens* and, dominating the shade circle of trees, *Ruellia tuberosa* and *Petireria alliacea*.

THORN SCRUB

Described by Beard (1944) as thorn woodland, the type is scrubby and usually open, or if closed, thin and sparse. The total flora is poor, mesquite (*Proposis juliflora*) making up 75% of the trees, the remainder being other members of the Mimosaceae and Caesalpiniaceae (Fig. 24). The slender, umbrella-like acacia trees are microphyllous, sparsely leaved, semi-deciduous and spiny. They may be 10-30 ft.

FIG. 24. *Prosopis juliflora* forming open thorn woodland on the alluvial plains.

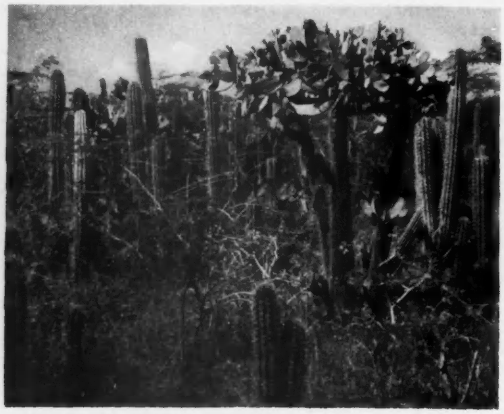


FIG. 25. Cactus-Thorn Scrub on the fringe of a salina. The cacti are *Cereus peruvianus* and *Opuntia spinosissima.* The thorns are *Acacia tortuosa* and *Prosopis juliflora.* The ground layer is a pure cover of *Batis maritima.*

high or windspread, stunted scrub. The conditions in Jamaica appear to be more unfavourable than those indicated by Beard for his type and most of the species show partial defoliation in the extreme dry period. While he recognized a separate climax in cactus scrub, this is regarded here as a littoral faciation.

Thorn scrub has been much modified by drainage operations, burning and shifting cultivation. At the present time, it is more characteristic of the coastal areas where it covers the infertile soils of mixed alluvium and saline clays. The climate is severe: high constant temperatures, and continuous sea breezes reduce humidity while rainfall is low and unevenly distributed so that, for 6 to 10 months of the year, it is never over 4 in. and often below 1 in.

Brockmann-Jerosch (1925) regarded the thorn scrub of Jamaica as an insular "facies" of the caatinga of tropical America and Brazil, while Harshberger (1911) erroneously likened it to chaparral. There is no doubt that much confusion has arisen because of its proximity to dry and arid limestone types with which it often mingles to form an ecotone with exchange of species, although a few are common to both. Floristic Composition.

Trees: *Prosopis juliflora, Acacia tortuosa, A. lutea, A. farnesiana, A. villosa, Haematoxylon campechianum, Caesalpinia vesicaria, C. coriaria,* and *Pithecellobium unguis-cati.* Less frequently: *Pisidia piscupula, Guaiacum officinale* and the introduced *Moringa oleifera, Tamarindus indica, Albizzia lebbeck* and *Leucaena glauca* are in association.

Shrubs are *Capparis ferruginea,* which is often abundant, *Cassia emarginata, Brya ebenus, Croton linearis, Capparis lanceolata* and the spiny ground bromeliad, *Bromelia pinguin.* Masses of xerophytic epiphytes include the bromeliads *Tillandsia recurvata* and *T. balbisiana* and the sinuous climbing cacti *Cereus triangularis* and *C. flagelliformis.*

The coastal faciation is often a low, sparse scrub, dominated by Prosopis with *Acacia tortuosa* and Pithecellobium and the characteristic cacti *Cereus peruvianus, Opuntia tuna, O. spinosissima,* and *Melocactus communis.* A ground cover of the halophytic herbs, *Batis maritima* and *Alternanthera ficoidea,* may be present (Fig. 25).

A cactus-thorn scrub, in which desert-like cacti, *Acacia tortuosa, Prosopis juliflora* and many species from the thorn woodland of the plains are blended together is found on sand spits of sufficient width and elevation. A good example is to be seen on the Palisadoes. Chapman (1944) regarded the acacia scrub as secondary in seral progression to a cactus scrub. However, although cacti, especially *Cereus peruvianus,* may become locally dominant, the climax is best regarded as an acacia thorn-scrub which includes cacti. The whole question of the relationship of cacti to this community requires further study.

To summarize, then, it may be said that the dry alluvial plains once supported several types of seasonal evergreen or deciduous forests. Man's activities have now produced successional communities which may lead to a disclimax of thorn thicket or thorn savanna dominated by *Acacia lutea.* The areas of mixed alluvium and saline clays have a characteristic thorn-scrub vegetation dominated by *Prosopis juliflora.* This community has a coastal faciation in which cacti predominate.

SWAMPS AND MARSHES

Beard (1944a) regards swamp and marsh formations as edaphic climaxes and defines marshes as seasonal swamps because of seasonal fluctuation in water level. His classification is a sound one and, applied to Jamaica, shows the following types:

a. Herbaceous swamp.
b. Mangrove woodland.
c. Palm-Sedge.
d. Marsh forest.

HERBACEOUS SWAMPS

The freshwater swamps of Jamaica are limited to a few small examples. They usually have an appreciable salt content. The upper reaches of the

short Ferry River, west of Kingston, may be taken as typical herbaceous freshwater swamp. The water here has 250 p.p.m. of salt and a pH of 8.0, and the vegetation is similar to such swamps occurring in Cuba and Porto Rico.

Floating and submerged plants are: *Pistia stratiotes, Hydrocotyle umbellata, Ceratophyllum demersum, Riccia fluitans,* Potamogeton, Myriophyllum, *Utricularia stellaris, Nymphaea alba, Eichornia crassipes, Azolla caroliana, Lemna minor* and Sagittaria.

Reeds and sedges include: *Typha angustifolia, Phragmites communis, Arundo donax, Echinodorus* sp., *Eleocharis* sp., *Mariscus jamaicensis, Cyperus giganteus* and *Cyperus* spp.

The more saline examples, which are the nearest tropical equivalent to temperate zone salt marshes, and bear some successional relationship to mangrove woodland are characterized by scattered mangroves, usually Rhizophora, *Acrostichum aureum* (the golden swamp fern), various tall reeds and sedges and a ground cover of fringing halophytes.

MANGROVE WOODLAND

This formation has a stable and uniform physiognomy throughout the Caribbean. The four New World species, *Rhizophora mangle, Laguncularia racemosa, Avicennia nitida* and *Conocarpus erecta* are all represented. The red mangrove, Rhizophora, is pre-eminently a seaward pioneer and possesses strut roots and the viviparous habit. Laguncularia, the white mangrove, and Avicennia, the black mangrove, have pneumatophores and are characteristic of the mud swamps. The button mangrove, Conocarpus, is found on dry land. It does not possess strut roots or pneumatophores, neither does it exhibit vivipary and is regarded by some as not being a true mangrove.

The authors agree with Chapman (1939, 1944) that the habitats for mangrove woodland in Jamaica are silt, sand, peat and coral reefs.

Silt Mangroves—Silt provides the most important habitat, and extensive areas of this kind are found associated with the protected river estuaries and the coastal margin of the alluvial plains. Mangroves play an important part in land elevation and seaward extension of the coast in these areas. The type of mud that occurs is variable and may be of fine, calcareous clay or have a coarser, sandy component. The organic content may be high in both cases, due to local conditions favouring peat formation. The marine "grasses" *Thalassia testudinum* (turtle grass) and *Cymodocea manatorum* (manatee grass) assist in the formation of marine deposits of mud and are of importance in preparing a bed for the mangrove seedlings.

Sand Mangroves.—A sandy habitat is found on many of the spits and cays as well as the sand shoals known as the Bogue Islands in Montego Bay.

Peat Mangroves.—Mangroves growing over deposits of peat were described by Chapman on the Palisadoes, the Fort Augusta sand-spit and in the Portland Bight. Davis (1940) found peat deposits in the mangrove swamps of Florida and, upon examination, the peat was seen to consist of the remains of Rhizophora and Avicennia. He also noted that along the outer edges of the swamps, Thalassia and Cymodocea, together with marine algae, play a part in the formation of peat soils. Recent borings in Kingston harbour near the Palisadoes have shown that there are extensive deposits of marine peat. This was examined by the authors and there is little doubt that it has been formed from the marine aquatics, especially Thalassia which is frequently uprooted and deposited by marine currents in large banks in the sheltered bays around the coast.

Reef Mangroves—This habitat includes the shallow reefs such as those occurring on the north coast and the boulders forming the shore of the rocky Cays. The vegetation is limited to scattered plants of Rhizophora and occasional Avicennia. The trees are held by their roots which penetrate into the holes and crevices of the coral, and between the boulders. Chapman regards them as adventives and the whole community as being unstable. Zonation within the mangrove community is, on the whole, poorly defined in Jamaica and this may be partly due to the limited tidal range which, at Kingston, fluctuates between 8-10 in. and is of short duration. Rhizophora requires shallow water for the establishment of its seedlings but, later, when strut roots are developed, the plants are able to extend out into several feet of water. Accordingly, this plant occupies the seaward fringe of the coastal mangroves and the deeper waters of the lagoons, salt ponds and inland swamps. Avicennia occupies the major part of the swamps behind the Rhizophora zone. It occurs in those areas periodically inundated by the tide as well as in the stagnant, saline and shallow water-flats rarely or never under tidal influence. Laguncularia is associated with Avicennia on the landward margin of the swamp where it may occasionally form a pure zone. Conocarpus, although invariably present on dry land fringing the mangrove swamp, is a member of other coastal communities as well. Davis regards Conocarpus as belonging to a transitional community or ecotone between the mangrove swamp and the strand communities. Chapman, however, from his observations in Jamaica, prefers to regard the Conocarpus associes as a seral community. Diagrams illustrating the principal successional stages in the mangrove swamps near Kingston are given by Chapman (1944).

Zonation is variable and its definition depends greatly upon the degree of protection, water level and salinity. The necessary edaphic conditions bringing about zonation are, however, effected by land elevation which will result in zonal advance of the mangrove woodland towards the open water. Finally, the mangroves will be superceded by an inland climax, usually regarded as climatic. In Jamaica, the inland climax which follows mangrove woodland is frequently a cactus thorn scrub, although salt flat communities (salinas) and brackish herbaceous swamps may also play a part. Thus, although there is a recent tendency to regard mangroves as a climax formation—for

example, Beard (1944a) classified Mangrove Woodland as an edaphic climax within his Swamp Formation series—the seral nature of the component zones should not be forgotten.

There are few associates of the mangroves, *Batis maritima, Salicornia ambigua, Acrostichum aureum* and *Alternanthera ficoides* are often present as undergrowth in the open woodland. On sand, *Sporobolus virginicus* may occur.

Salinas, or salt flats, frequently occur as a landward fringe of the mangrove woodland on the south coast. They are to be found where the substratum is a heavy saline clay. Such areas are sufficiently low-lying to be inundated by the sea during storms or exceptionally high tides. On the other hand, they are sufficiently elevated to prevent normal tidal inundation. The clay soil tends to retain the surface water but the evaporation rate is so high that there are long periods of the year when the surface is dry. However, due to evaporation, salinity is high. In some cases, salt crystals can be seen on the surface. Such areas are bare of vegetation but, more frequently, the salinity, while high, is not sufficient to prevent the extreme halophyte *Batis maritima* from being present. This plant frequently forms a pure cover. Occasional associates are *Sesuvium putulacastrum* and *Salicornia ambigua*. Where salinity falls, *Heliotropium curassavicum* and *Portulacca oleracea* may be present. The landward side of the larger salinas gradually pass over to cactus thorn scrub (Fig. 26).

The processes concerned with the formation of salinas need further attention. They may be formed from salt ponds by evaporation, as outlined on page 374 and then will never have been occupied by mangroves. On the other hand, they may be produced as a result of drying out following artificial drainage, change in the course of rivers or elevation of the land in relation to sea level. In such areas, the salinas may have formerly supported mangroves. Chapman noted that the salinas in the Hunts Bay region contained old stumps of Avicennia and suggested that alterations in the course of the Rio Cobre, which are known to have occurred, have resulted in drying out and subsequent death of the Avicennia community, formerly occupying the present salinas.

Fig. 26. A large salina at Port Henderson covered by *Batis maritima*. Occasional stunted bushes of Laguncularia are present. Thorn scrub and cactus-thorn scrub are seen in the background.

PALM-SEDGE MARSH

The largest swamp area of Jamaica is really a sedge marsh with scattered palms. This covers almost the whole of the low-lying flood plains of the Black River, the delta being some 100 sq. mi. in extent. During the rainy season, it is inundated with freshwater from the swollen rivers, whilst, in the dry season, much of the higher ground dries out to marsh.

The many tributaries of the Black River find their confluence a mile or so above the mouth, this part being known as Broadwater. Above this there are two main branches, the lesser being of dark, sluggish water and open to boats for some five miles. The main river branch is navigable for some 30 mi., flows more swiftly and is often muddy yellow with silt. The river is tidal and brackish for about five miles from the sea. The vegetation shows two aspects: a marginal zone along the river banks and the marsh area inland. The west bank of Broadwater has a dense border of mangroves, chiefly *Rhizophora mangle*, up to 30-40 ft., in height; Lanuncularia and Avicennia are occasional. Rhizophora may continue for 6 mi. up the river, although it is reduced in height and becomes less and less frequent. The mangroves are correlated closely with the current and formation of silt banks, being strictly confined to the inner bends of the river. Where the river takes a sharp turn and silt is deposited on the opposite bank, the mangrove belt also changes sides. Opposite the mangroves, there is a zone of *Typha angustifolia* and *Phragmites communis*. In the absence of mangroves it is usually Typha which is dominant and, here, Typha has the same distributional pattern in relation to silt deposition as had Rhizophora. This marginal fringe has also the following species: *Acrostichum aureum, Jussieua suffruticosa*; and the climbers: *Ipomea fastigiata, Ipomea carnea, Aristolochia trilobata* and *Mikania micrantha*.

Close to the banks, the floating or submerged flora includes: Nymphaea, Sagittaria, Eichornia and others of the freshwater swamps.

By far the greater portion of the Black River area is a sedge marsh which is spread out between the many branches of the river. This is dominated by an almost pure cover of the large *Cyperus giganteus* although other Cyperus and Carex species are present. Scattered throughout this area, are groups of the royal palm, *Roystonea princeps*, up to 35 ft., and endemic to this area of Jamaica. Nearer the sea, this is joined by *Calyptronoma swartzii*.

MARSH FOREST

Beard (1946) described marsh forest on alluvial terraces in Trinidad. The same association is known from British Guiana but does not occur in the Lesser Antilles. Marsh forest (Fig. 27) in Jamaica is limited to a few square miles of the upper reaches of the Black River and may also occur further along the coast near Cave. Typically developed on the higher ground where two tributaries meet, the forest is subject to periodic inundation. The floor remains wet and muddy after rain.

FIG. 27. Marsh Forest bordering the Black River. The canopy tree is *Symphonia globulifera* with a lower storey of *Grias cauliflora* and the palms, *Roystonea princeps* and *Calyptronoma swartzii.*

The canopy is closed at about 30 ft., and made up of palms (*Roystonea princeps, Calyptronoma swartzii*) which are also members of the palm marsh. The dominant tree is hog gum (*Symphonia globulifera*) with aerial roots and an exudate of yellow gum when cut. Symphonia frequently forms the emergent layer. *Grias caulifera* is a very characteristic small tree with large pendant leaves. Other trees, many of which have invaded from neighbouring communities, are: *Calophyllum jacquinii, Terminalia latifolia, Piscidia piscipula, Ficus* spp., *Haematoxylon campechianum* and *Spondias monbin.* Buttress roots are not characteristic.

Epiphytes are aroids and orchids but bromeliads are rare. Colocasia and ferns form a ground layer.

SHALE

VEGETATION ON THE LOWER SHALE HILLS

Some of the most cultivated aspects of Jamaica are the "shale" soils of the lower hills and valleys. There are three shale regions, the Blue Mountains in the east which proceed to high elevations, and the central and western regions, both of which are below 2,500 ft., Bull Head (2,782 ft.) in the central region being an exception.

Geologically, two major series are included: the Carbonaceous shales of the Lower Eocene (black shales, coarse conglomerates, limestone and sandstone) and the Cretaceous shales. These latter are red and purple shales, tuffs, breccias and conglomerates interbedded with fossiliferous limestone of the Upper Cretaceous. These rocks produce a complex of local soil types that is included under the term "shale".

Most of the "shale" soils are very porous but, in Jamaica, the consequent free drainage is offset by the high rainfall over the regions where they occur. The profile is often degraded or truncated, much of the area being of "forest soils" which have been badly eroded following deforestation and poor agricultural practices.

The lower shales were originally covered with a sparse, mesophytic forest but the exact nature of this forest is now a matter of conjecture from the remnants still to be found in the lower valleys following the stream beds. On the St. Andrew slopes of the Blue Mountain system (Fig. 28) there is a rather sparse forest of large spreading trees and tall spindly shrubs forming a thin canopy broken by emergent cotton trees. This extends up the ravines but, elsewhere, soon tails off into open grassland with a few low hardy shrubs and scattered trees. Much of the present vegetation of the open slope is due to man's interference. The upper soil layers have been rapidly lost after deforestation, continued burning and shifting patchwork cultivation. This has been greatly accelerated by surface erosion due to the steep topography. In St. Andrew, and best seen on the slopes of the Port Royal ranges, this has led to a characteristic hill savanna of guinea grass and mango trees where once there was continuous cover (Fig. 29). *Bambusa vulgaris* with large feathery branches is common in some areas (Fig. 30).

FIG. 28. Remnant mesophytic forest of the lower shale valleys of St. Andrew. Dominant trees are Ceiba, Cecropia, Cedrella, Pithecellobium and the introduced *Samanea saman.* Note the steep slopes in the distance from which the forest has been removed and which now support grassland with scattered shrubs and trees.

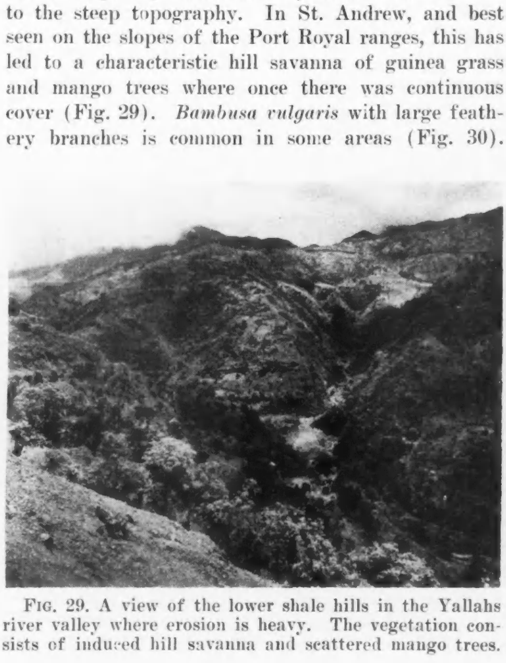


FIG. 29. A view of the lower shale hills in the Yallahs river valley where erosion is heavy. The vegetation consists of induced hill savanna and scattered mango trees.

Fig. 30. Bamboo brake on the shale hills.

Common among the introduced and cultivated trees are: *Mangifera indica, Meliococca bijuga, Artocarpus integrifolia, A. incisa, Cola acuminata, Theobroma cacao, Cocos nucifera, Gliricidia sepium, Bambusa vulgaris, Tamarindus indica, Samanea saman, Eugenia jambos, Inga vera, Anona reticulata, Albizzia lebbeck, Eugenia malaccensis;* the trailing "Spanish moss" *Tillandsia usneoides* is a characteristic epiphyte.

The remnant forests of the lower stream valleys include the following trees:

Ceiba pentandra
Cecropia peltata
Cedrela odorata
Pithecellobium arboreum
Chlorophora tinctoria
Zanthoxylum flavum
Ochroma pyramidale
Chrysophyllum ovaliforme
Catalpa longissima
Ficus suffocans
F. wilsonii
Prunus myrtifolia

On the slopes, the sparser forest of smaller trees contains:

Andira inermis
Hura crepitans
Bursera simaruba
Guazuma ulmifolia
Spondias monbin
S. purpurea
Comocladia pinnatifolia
Spathelia sorbifolia
Bauhinia divaricata
Crescentia cujete
Amyris balsamifera
Nectandra sanguinea
N. antillana
Cordia gerascanthoides
Coccoloba laurifolia
Celtis trinervia
Trema micrantha
Byrsonima coriacea
Pimenta officinalis
Guarea glabra
Clusia rosea
Drypetes lateriflora
Picramnia antidesma
Heteropteris laurifolia
Matayba apetala
Brya ebenus
Senecio discolor

The ground flora includes:

Bletia purpurea
Bidens cynapiifolia
B. pilosa
Asclepias nivea
Vernonia divaricata
Iresine paniculata
Piper umbellatum
P. amalago
P. aduncum
Peperomia verticillata
Pilea microphylla

and the ferns:

Asplenium pumilum
Aneimia underwoodiana
A. hirsuta
Dryopteris pedata
D. resinifera
Blechnum unilaterale
Gymnopteris rufa
Lygodium volubile
Notholaena trichmanoides
Trismeria trifoliata

The open banks have quite a rich and characteristic moss flora with such species as:

Breutelia jamaicensis (Mitt) Jaeg.
Pleuropus bonplandii (Hook) Broth.
Brachythecium steropoma (Spruce) Jaeg.
Papillaria nigrescens (Hedw) Jaeg.
Anoectangium euchloron Schwaegr.
Philonotis glaucescens (Hornsch) Par.
Bryum crugeri Hpe.
B. argenteum Hedw.
B. truncorum Brid.
Calliergonella cuspidata (Hedw) Loeske
Campylopus introflexus (Hedw) Brid.
Haplocladium microphyllum (Hedw) Jaeg.
Meteoriopsis remotifolia (Hornsch) Broth.

Others found in the moist forest remnants are:

Helicophyllum tortuatum (Hook) Brid.
Entodon macropodus (Hedw) C. M.
Fissidens similiretis Sull.
Helicodontium capillara (Hedw) Jaeg.
Samatophyllum galipense C. M.
Squamidium nigricans (Hook) Broth.

Montane Communities

Lower Montane Rain Forest

A typical lowland tropical rain forest cannot be recognized in Jamaica to-day. The closest approach is seen in the type of rain forest occupying a narrow zone of the lower northern slopes of the Blue Mountain range and the western slopes of the John Crow Mountains. Annual rainfall in the former regions is well over 100 in. while 275 in. has been recorded at Millbank in the vicinity of the latter. There is no marked dry season. On the Blue Mountain range, much of this original forest has been cleared and that which remains occupies the more inaccessible slopes and gradually merges into Mist Forest at altitudes above 3,500 ft. In the east, Corn Puss Gap at 2,000

ft., and Cuna Cuna Gap at 2,500 ft., represent the lowest points at which this type of forest has been observed on the Blue Mountain range. The western slopes of the John Crow Mountains support rain forest from 1,500 ft.-2,500 ft. Above this, it thins out to a mixed palm brake and mist forest, and finally and abruptly to elfin woodland. The John Crow Mountains form the eastern boundary of the low-lying, humid Rio Grande valley. It is in this valley that the remnant vegetation of tree ferns, Helicornias and aroids clearly indicate a locality where lowland tropical rain forest may have flourished in the past and spread up to the type now to be described.

We have called this community Lower Montane Rain Forest since it resembles closely the type so named by Beard for the lesser Antilles and Trinidad. It may be thought of as a variant or facies of lowland tropical rain forest from which it appears to differ in the following respects. The main canopy is lower, being here at 80 ft. There is a less well-defined stratification, few trees with buttresses, and lianes and epiphytes, although present, are not abundant.

The stands of lower montane rain forest which have been examined are all on sloping ground and the substratum is limestone in the case of the John Crow Mountains and shale on the Blue Mountains.

Structure.

A profile diagram of a typical area at 1,800 ft., on the western slopes of the John Crow Mountains is given in Fig. 31. Here is a mixed forest with occasional huge emergent trees of *Psidium montanum* reaching up to 120 ft. and having a girth of 9-11 ft. The main canopy, which is not dense, is at 60-80 ft., and the girth varies from 4-6 ft. A somewhat ill-defined lower layer occurs from 30-50 ft., and may include palms. Tree ferns are rare.

A profile diagram (Fig. 32) of the forest taken near Cuna Cuna Gap at 2,500 ft. also shows a closed canopy from 60-80 ft. but it consists almost exclusively of *Calophyllum jacquinii* (Santa Maria). There is an ill-defined sub-canopy from 40-55 ft., and a lower layer from 10-30 ft. The relatively steep slope here does not aid the clear demarcation of the lower strata.

It is from such areas as these that the following preliminary description of this type of forest oc-

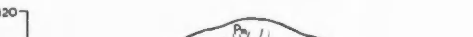


FIG. 31. A profile diagram of Lower Montane Rain Forest measured in the western slopes of the John Crow Mountains at 1,800 ft. The diagram represents the trees present in a belt 100 ft. long and 25 ft. wide.

KEY TO SYMBOLS: Al. *Alchornea latifolia* (Jumba); Cj. *Calophyllum jacquinii* (Santa Maria); Cs. *Calyptronoma swartzii*: E. *Eugenia* sp. (Rodwood). Ep. *Exothea paniculata* (Wild Ginep); F. *Ficus* sp.; Fo. *Faramea occidentalis* (Wild coffee); Gg. *Guarea glabra* (Alligator, Wild akee); Ma. *Matayba apetala* (Wannika); N. *Nectandra* sp. (Sweetwood); Pa. *Pithecellobium alexandrii* (Shadbark); Pm. *Psidium montanum* (Mountain guava); R. *Rubiaceous* sp.; Sg. *Symphonia globulifera* (Hog gum); Tr. *Trophis racemosa* (Ramoon).

FIG. 32. Profile diagram of Lower Montane Rain Forest measured at Cuna-Cuna Gap in the Blue Mountain Range. The diagram represents the trees present in a strip 100 ft. long and 25 ft. wide.

KEY TO SYMBOLS: Al. *Alchornea latifolia* (Jumba); Cj. *Calophyllum jacquinii* (Santa Maria); Co. *Clethra occidentalis*; Cy. *Cyathea* sp.; D. *Dipholis* sp. (Bullet wood); E. *Eugenia* sp. (Rodwood); Ep. *Exothea paniculata* (Wild Ginep); Gg. *Guarea glabra* (Alligator, Wild akee); Ha *Hedosymum arborescens*; He. *Hernandia* sp. (Womanwood); M. *Melastome* sp. (Soapwood); Ma. *Matayba apetala* (Wannika); Me. *Mimusops excisa* (Wild naseberry); 'Mw' Unidentified ('Milkwood'); N. *Nectandra* sp. (Sweetwood); P. *Psychotria* sp.; Sj. *Sapium jamaicense* (Blindeye); Uk. Unidentified.

curring in Jamaica is built up. Apart from occasional and widely spaced emergents such as *Psidium montanum, Symphonia globulifera* and *Ficus suffocans* reaching up to 120 ft., the main canopy extends from 60-80 ft. The lowermost branching of this layer is at 60 ft., and a wide-spreading flat-topped crown is developed. Spacing of the trees may be close but variation occurs due to soil depth and drainage.

The canopy is often dense where there is a single dominant such as Santa Maria, but more open in the mixed forest. The lower tree layer is similarly variable in density between 30-50 ft., and with ill-defined stratification.

The shrub layer from 10-20 ft. is usually sparse, due to the poor light, and is represented by spindly shrubs of the Rubiaceae and Melastomaceae, together with *Eugenia, Piper* and *Helicornia* species.

The field layer is predominantly of ferns, tree seedlings and bryophytes.

Among the trees a few, such as Psidium and Ficus, show buttressing while stilt roots are seen in Symphonia which, together with Ficus and Sapium, has latex. The tree fern, Cyathea, is the only thorny member. Tree ferns, and more especially palms, characterize the lower strata of the forest.

Lianes are not abundant but there are many small vines, including Smilax, several aroids, Marcgravia and other climbing herbs and ferns.

Epiphytes are represented by bromeliads which are here limited to the higher tree branches at 60-70 ft.; ferns, bryophytes and orchids occur at the shrub level.

All the tree species are evergreen with simple leaves, except in the case of Matayba, Pithecellobium and Guarea. Leaf size falls into Raunkiaer's mesophyll group.

The forest floor is of moist soil, rich in humus and organic litter, usually with a cover of ground ferns and Santa Maria (Calophyllum) seedlings. Bryophyte societies occur on small rocks and fallen branches with Thuidium and Leucobryum as the dominants.

Floristically, there is some relation with the wet limestone forest.

Emergent trees:
- *Symphonia globulifera*
- *Psidium montanum*
- *Ficus suffocans*

Trees of the main canopy:
- *Calophyllum jacquinii*
- *Matayba apetala*
- *Nectandra antillana*
- *Clethra occidentalis*
- *Exothea paniculata*
- *Dipholis* sp.
- *Cyrilla racemiflora*
- *Prunus occidentalis*

Sub-canopy trees:
- *Guarea glabra*
- *Pithecellobium arboreum*
- *Sapium jamaicense*
- *Nectandra sanguinea*
- *N. coriacea*
- *Eugenia disticha*
- *E. monticola*
- *Hufelandia pendula*
- *Oxandra laurifolia*
- *Ocotea martinicensis*
- *Hernandia catalpifolia*
- *Alchornea latifolia*
- *Dipholis* spp.
- *Cecropia peltata*
- *Calyptronoma swartzii*

Shrub layer: Melastomaceae:
- *Miconia laevigata*
- *Ossaea sperifolia*
- *Conostegia superba*
- *Blakea trinervia*

Rubiaceae:
- *Psychotria pedunculata*
- *P. nervosa*
- *Faramea odoratissima*

Also:
- *Gilibertia ovalifolia*
- *G. arborea*
- *Rheedia pendula*
- *Hedyosmum arborescens*
- *Columnea hirsuta*
- *Lacistema aggregatum*
- *Rytidophyllum grande*
- *Piper nigrinodum*
- *P. discolor*
- *P. scabrum*
- *Helicornia caribaea* adds a distinctive note.

Tree ferns, which are not frequent in this forest, are:
- *Cyathea tussacii*
- *C. grevilleana*
- *Ctenicis villosa*
- *Alsophila swartsiana*
- *A. aspera*

The field layer:
- *Besleria lutea*
- *Pachystachys coccinea*
- *Lobelia acuminata*
- *Gryotaenia microcarpa*
- *Peperomia hispidula*
- *P. crassicaulis*
- *Scybalium jamaicensis*, the root parasite.

Ground ferns:
- *Asplenium cuneatum*
- *Diplazium faydenii*
- *D. pectinatum*
- *Camptodium pedatum*
- *Bolbitis pergamentacea*
- *B. aliena*
- *B. nicotianaefolia*
- *Dryopteris gemmipara*
- *D. deltoidea*
- *D. decussata*
- *Thelypteris serrulata*
- *Pteris hexagona*
- *Tectaria incisa*

Polybotrya cervina
Nephrolepis rivularis
Danaea jenmanii
D. nodosa

Ground mosses:
Thuidium acuminatum Mitt.
Leucobryum antillarum Schp.
Epipterygium wrightii (Sull.) Lindb.
Leucoloma serrulatum Brid.
Fissidens elegans Brid.
F. mollis Mitt.
F. polypodioides Hedw.
Lepidopilum polytrichoides (Hedw.) Brid.

Epiphytes and climbers:
Begonia glabra
Philodendron tripartitum
P. lacerum
P. cordatum
Smilax domingensis
Marcgravia brownei
Schradera involucrata
Elleanthus capitatus
Dichaea graminea
Epidendrum fragrans

Epiphytic and climbing ferns:
Trichomanes scandens
T. crispum
T. hymenophylloides
T. rigidum
T. holopterum
T. osmundoides
Hymenophyllum crinitum
H. hirtellum
H. hirstum
Polypodium mollissimum
P. jubaeforme
P. lycopodiodes
P. exornans
Elaphoglossum simplex
E. petiolatum
Polytaenium feei

Epiphytic mosses:
Octoblepharum albidum Hedw.
Lepyrodontopsis trichophylla (Sw.) Broth.
Pireela filicina (Hedw.) Card.
Pilotrichum amazonum Mitt.
Meteriopsis remotifolia (Hornsch) Broth.

MONTANE SCLEROPHYLL

At about 2,500 ft. on the St. Andrew (leeward) slopes of the Blue Mountain ranges. the vegetation changes quite suddenly and abruptly to a sclerophyll zone which continues up to 4.000 ft. This zone would appear to be unique in the West Indies, although such dry belts at higher altitudes are not unknown elsewhere in the tropics. There is a similar aspect called "ceja" on the Andes and such belts are also said to occur in Borneo and Ceylon. The montane sclerophyll has two aspects. At the lower altitudes it consists of a low open shrubby community under the periodic influence of shifting cultivation. Above this is a less disturbed thicket of small trees and shrubs which extends up to the Mist Forest.

The lower sclerophyll belt is of low, bushy shrubs, sparse in cover and scant of foliage. Xeromorphic features are characteristic, the most common being small, hard, thick leaves.

Two very characteristic shrubs restricted to this community are the mountain broom, *Baccharis scoparia,* with minute, green leaves and green, twiggy stems and *Dodonea viscosa,* a small hardwood shrub up to 12 ft. *Dodonea viscosa* is a common lowland coastal species found throughout the Pacific. In Jamaica, it is restricted to this inland elevated community.

Other small shrubs present are:
Clusia rosea
Lantana involucrata
Eugenia spp.
Senecio discolor
Vernonia divaricata
Solanum verbascifolium
Lyonia jamaicensis
Heterotrichum umbellatum
Ascyrum hypericoides

Hard, stiff-leaved pteridophytes are typical of the ground layer, notably:
Pteridium arachnoidium
Gleichenia jamaicensis
Polypodium thysanolepis
Lycopodium cernuum

At this level, guinea grass (*Panicum maximum*) gives way to molasses grass (*Melinis minutiflora*), also an introduced species which is spreading fast and becoming characteristic of this region.

A number of small trailing woody herbs are very characteristic and include:
Chusquea abietifolia—the climbing bamboo
Relbunium hypocarpium
Manettia lygistum
Coccocypselum herbaceum
Micromeria obovata

Herbs include:
Crotalaria retusa
Bidens pilosa
Cordia cylindrostachya
Pavonia rosea
Bryophyllum pinnatum
Flemingia strobilifera
Leianthus longifolius
Gnaphalium americanum

The lichens Usnea and Cladonia and terrestrial mosses are also present.

Moist shaded banks support *Pilea microphylla, Selaginella* spp., *Achimenes coccinea* and other hygrophilous plants.

The low, bushy sclerophyll merges into a dry, evergreen thicket at the higher altitudes (3,000-4,000 ft). This does not correspond to the montane thicket described by Beard (1949) for the Lesser Antilles, which would seem to be equivalent to our Mist Forest. The environment of the sclerophyllous thicket recog-

nised on the south slopes of the Blue Mountains is much drier than Mist Forest with which it has, nevertheless, some floristic affinity. The canopy is more open and from 20-30 ft., high. Dominant among the small trees and tall, slender shrubs are:

Cyrilla racemiflora
Vaccinium meridionale
Clethra occidentalis
Eugenia spp.
Viburnum villosum
Persea alpigena
Coccoloba laurifolia
Clusia rosea
Guettardia argentea
Nectandra patens
Bocconia frutescens

Many of the members belong to the Ericales and Myrtales.

The sclerophyll belt as a whole is rather difficult to explain. In the lower aspect, a number of lowland representatives reappear, such as Lantana, Bryophyllum and Solanum. These belong to secondary growth "ruinate" areas of the dry limestone and alluvium, but occur here together with the bona fide sclerophylls such as Baccharis, Pteridium and Gleichenia.

Grevillea robusta and Eucalyptus, both native to the drier regions of Australia do well here. Drought, however, is not evident even allowing for the sharp decrease in rainfall when compared to the north slopes, where, at the corresponding level, remnants of lower montane rain forest occur.

Brockman-Jerosch (1925) suggested that the factor of most importance for the sclerophyll belt was that of lowered humidity. It is true that the trade winds are depleted of moisture by the time they reach the southern slopes and that the sclerophyll belt does not enter the Blue Mountain mist level. Shreve (1914) found a continued high humidity of 95% for the north ravines but, at Cinchona on the south side, a fluctuating value from 50% to 90%. Evaporation rates were four to five times greater than those of the north slopes. The relative transpiration rates of Dodonea, a typical sclerophyll shrub, was here double that of Clethra from the mist forest where high humidity retarded transpiration. His data would indicate that humidity and evaporation—transpiration ratios are the controlling factors for the sclerophyll.

Ecological considerations provide another line of attack to this problem. At first it is difficult to see anything of a seral nature in the sclerophyll belt. However, on the wet Portland slopes at 2,500 ft., there are minor areas which, from their species, are very reminiscent of the sclerophyll. Such small bushes such as Gleichenia, Pteris and Baccharis occur with the trees Clethra, Viburnum, Coccoloba and Nectandra. Here, however, there is ample evidence of past clearing and burning and the vegetation is undoubtedly seral. Again, in the central shale region on Bull Head (1,782 ft.), where there was once a lower montane rain forest of Santa Maria, there is now a type of secondary community which includes: Cyrilla, Clethra, Eugenia, Clusia, Persea, *Myrica microcarpa*, Lyonia, Baccharis, *Miconia albidans* and *Clidonia strigillosa* together with the ground herbs: Gleichenia, Lantana, and Pteridium with the grasses *Andropogon virginicus* and *Melinis minutiflora.*

These facts indicate that the lower sclerophyll belt is a second growth community which, if left undisturbed, might eventually lead to sclerophyllous thicket or, on the wetter northern slopes, to lower montane rain forest. Such development may very well be a long-term process in regions such as this where leaching and erosion have followed repeated burning and clearing practised for shifting cultivation. These processes not only prevent regeneration of the trees but have completely changed the edaphic conditions. The fertile surface layers of the soil have gone and, on the steeper slopes, the whole topsoil has been washed down the mountainside. Colonization is by light-seeded weeds and shrubs. There are large patches in the sclerophyll belt where an almost pure cover of either *Melinis minutiflora* or *Gleichenia pectinata* prevails as a result of repeated burning.

MONTANE MIST FOREST

One of the few remaining retreats of original vegetation in Jamaica is to be seen in the montane mist forest clothing the upper reaches of the Blue Mountains which form the central mountain system in the eastern end of the island.

The mist forest may be recognised from about 4,500 ft. upwards together with an elfin woodland aspect. Reference to this forest is found in most accounts of visiting botanists. Ørsted (1857) thought it poor and monotonous in character; Boergensen (1923) "the most peculiar vegetation imaginable," and Brockman-Jerosch (1925) wrote of the confusing abundance of species and the rich plant life in a muggy, glasshouse atmosphere. The fullest account is in Shreve's monograph (1914).

This type of forest has been described throughout Central America and the Caribbean islands. There is little doubt that mist, which cuts down the light and increases humidity, is a far more important factor than rainfall. Pittier (1939) has described the close association in the Venezuelan Andes between such forest and the mist belt. Carr (1949) alludes to the tear-like condensation of water on the trees of the cloud forests of Honduras and Miranda & Sharp (1950) to the fog forest in Eastern Mexico. Gleason & Cook (1927), describing the mossy forests of the Luquillo forests of Porto Rico, describe the peaks as wrapped in cloud which "raises humidity, brings about daily rainfall and reduces the sunshine to short intervals."

In the Blue Mountains of Jamaica, the upper ridges are enveloped daily in mist from 10 A.M.-4 P.M., that is for a period of at least 6 hours (Fig. 33). The mist persists even during rain but much of the moisture, enabling the hymenophyllous ferns and hygrophilous plants to flourish, is due to condensation.

The soil is extremely porous and a high proportion

FIG. 33. General view showing the Mist Forest of the Blue Mountains. In the lower foreground is a plantation of Blue Mahoe (*Hibiscus elatus*).

FIG. 34. An open aspect of Montane Mist Forest at St. Catherine's Peak. The canopy trees are Cyrilla, Alchornea and Podocarpus. Tree ferns, shrubs and epiphytes are conspicuous.

of the rainfall is rapidly drained off, due to the steep slopes. The rainfall is distributed in light showers but actual figures are reduced in significance, due to the low evaporating power of the air.

Shreve concluded that sunlight was cut down to one quarter of the normal, the nights being clear but mist forming 5-15 minutes after sunrise each day. He estimated the daily duration of mist as a percentage of the total daylight hours and gives the following figures for the leeward and windward slopes above 4,500 ft.

	North.	South.
Feb, July, August	30%	10%
Other months	70%	30%

Working on the physiological aspects, Shreve was able to correlate a daily march of transpiration rates with mist formation.

Variation in the structural and floristic composition of the mist forest is wide and almost entirely correlated with degree of exposure. Shreve describes the forest of the ravines, the ravine slopes and the ridges. The chief variation is between that of the deep, sheltered, ravines and that of the exposed ridges. The main structural difference is in the canopy which, with progress towards the exposed ridge, becomes lower, open and more uniform, whilst the species in shrub and ground layers change to the more xerophytic ones. Shreve showed that, on the exposed ridges, air movement lowered the humidity greatly.

STRUCTURE—The mist forest is low-canopied, wet and misty. The evergreen trees with sombre dark-green, broad leaves are associated with an abundance of small, melastomaceous and rubiaceous undershrubs, pteridophytes and bryophytes (Fig. 34). In both structure and floristics, it shows many temperate forest features.

The profile diagram (Fig. 35) is for mist forest at 4,200 ft. near Catherine's Peak on a range subsidiary to the Blue Mountains.

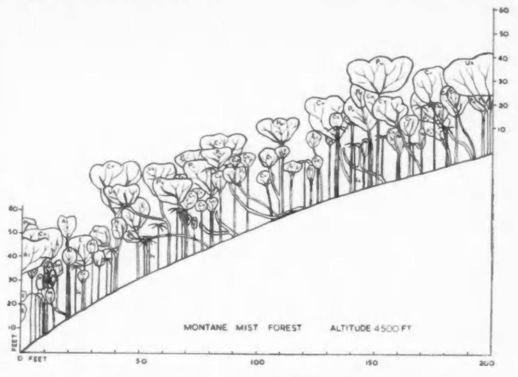


FIG. 35. Profile diagram of Mist Forest measured at 4,500 ft. in the Blue Mountain Range. The diagram represents the trees present in a belt 200 ft. long and 25 ft. wide.

KEY TO SYMBOLS: Al. *Alchornea latifolia* (Jumba); Cl. *Clusia* sp. (Wild Fig); Co. *Clethra occidentalis*; Cr. *Cyrilla racemiflora* (Bloodwood, Beetwood); Cy. *Cyathea* sp.; E. *Eugenia* sp. (Rodwood); Ha. *Hedosymum arborescens* Sw.; M. *Melastomaceous* sp. (Soapwood); N. *Nectandra* sp. (Sweetwood); Pu. *Podocarpus urbani* (Yacca); So. *Solanaceous* sp.; Uk. Unidentified.

Emergent trees are few, the canopy at 40-50 ft. being uneven and somewhat open. A sub-canopy of varying density can be recognised at 30 ft. The shrub layer at 10 ft. is far more scattered while the field layer is a close and often luxuriant cover of herbs, ferns and bryophytes.

The dominant trees of the canopy, Podocarpus, Cyrilla and Alchornea are spaced at about 10 ft. and average 2 ft. 6 in. in girth. Most tend to be tall and spindly, with bushy crown branching. Cyrilla is frequently inclined in the direction of the slope. Shreve was of the opinion that this leaning indicated erosion movement of the shallow topsoil. It appears, however, that there are other factors such as wind exposure, growth towards light where trees have been felled by hurricanes etc. Similar features can be seen in Beard's profiles for montane rain forest in Trinidad.

Tree ferns are frequent, adding character, but palms are absent from this community in Jamaica. Compound leaves are seen in Brunellia, Wienmannia and Guarea, but generally the leaves are simple, often coriaceous, evergreen and small. Podocarpus and Cyrilla have flaky bark, but buttress roots and cauliflory (seen to a limited extent in Solanum and Mecranium) are generally absent. Clusia has aerial roots and begins life as an epiphyte. Lianes are rare but are represented by climbers up to 25 ft. such as Smilax, Marcgravia and Schradera. Epiphytes do not extend much above 15 ft. and include shrubs, bromeliads, orchids, ferns and bryophytes. Many are to be found again as members of the ground flora on fallen debris.

FLORISTIC COMPOSITION—Floristically, the montane mist forest is simple, the same species occurring in the different aspects with great uniformity.

The dominants are *Podocarpus urbani* and *Cyrilla racemiflora* and this leads logically to naming this montane community the Podocarpus-Cyrilla association.

Associated with the canopy layer are:

Podocarpus urbani
Cyrilla racemiflora
Alchornea latifolia
Clethra occidentalis
Brunellia comocladifolia
Solanum punctulatum
Laplacea haematoxylon
Ficus harrisii
Guarea glabra

The sub-canopy of under trees includes:

Clusia havetioides
Eugenia biflora
E. fragrans
Podocarpus urbani
Clethra occidentalis
Cyrilla racemiflora
Vaccinium meridionale
Gilibertia arborea
G. nutans
Acnistus arborescens
Weinmannia pinnata
Sciadophyllum brownei

The following less frequently occurring trees, are characteristic of differing aspects:

Juniperus barbadensis
Psidium montanum
Myrica microcarpa
Garrya fadyenii
Citharexylum caudatum
Nectandra patens
Dipholis montana
Rapanea ferruginea
Viburnum villosum
Turpinia occidentalis
Lyonia jamaicensis
Rhamnus sphaerosperma
Eugenia marchiana
Eroteum theoides

The shrub layer includes many species. Not all of these will be found in any one area as this layer shows the greatest variation with aspect. The species are:

Hedyosmum arborescens
Psychotria corymbosa
P. brachiata
P. brownei
Cephaelis elata
Palicourea crocea
Meriania purpurea
M. leucantha
Heterotrichum umbellatum
Miconia rubens
M. quadrangularis
M. dodecandra
Mecranium purpurescens
M. virgatum
M. amygdalinum
Tournefortia cymosa
Ilex montana
Myrica microcarpa
Columnea hirsuta
Ocotea jamaicensis
Hufelandia pendula
Acalypha virgata
Cestrum hirtum
Datura suaveolens
Bocconia frutescens
Boehmeria caudata
Piper hispidum
P. otophyllum
P. arboreum

The field layer includes the following herbs: *Begonia acutifolia*, many Peperomias and Pileas, *Lobelia assurgens, Besleria lutea, Panicum palmifolium, Uncinia hamata*, and *Rhynchospora eggersiana*. Many introduced, temperate species found on the open paths belong to such genera as: *Plantago, Rumex, Ranunculus* and *Fragaria*.

Ferns are too numerous to mention in detail. Among the ground ferns are:

Danea jamaicensis
Gleichenia pectinata
Diplazium centripetale
D. brunneo-viride
D. costale
D. heteroclita
Cryopteris denticulata
Dennstaedtia globulifera
Elaphoglossum eggersii
Asplenium pramorsum
A. harpeodes
A. alatum
A. radicans
Blechnum polpodioides
B. lineatum
B. jamaicense
Nephrolepis pectinata
Cystopteris fragilis

Tree ferns:

Lophosoria quadripinnata
Marrattia alata

Ortheopteris domingensis
Cyathea nigrescens
C. tussacii
C. pubescens
C. armata

Epiphytic ferns: *Polypodium loriceum* is common in mist forest. *Grammitis,* with 22 species occurring as epiphytes on mossy tree trunks and branches, is a characteristic genus of the montane formations. *Grammitis serrulata* is very frequent.

The filmy ferns, *Hymenophyllum sericeum, H. polyanthos* and *H. lanatum* are frequent to abundant, as well as many *Trichomanes* spp.

Climbers and scramblers, some of which are epiphytic shrubs:

Passiflora penduliflora
Maurandia erubescens
Marcgravia brownei
Cassia viminea
Schradera involucrata
Blakea trinerva
Solandra grandiflora
Metastelma fawcettii
M. atrorubens
Begonia glabra
Manettia lygistrum
Cionosicys pomiformis
Smilax celastroides

True epiphytes are the bromeliads, *Thecophyllum sintensii, Tillandsia incurva,* Hohenbergia and *Guzmania* spp., and the orchids: *Dichaea graminea, Dichaea glauca, Lepanthes concinna, L. tridentata, L. concolor, Epidendrum verrucosum, Liparis elata* and *Stelis ophioglossoides.*

Mosses, terrestrial and on logs:

Campylium chrysophyllum (Brid.) Bryhn.
Pleuropus bonplandii (Hook.) Broth.
Syrrhopodon lycopodioides (Sw.) CM.
S. gaudichuadii Mont.
Pilopogon gracilis (Hook.) Brid.
Ditrichum rufescens (Hpe.) Broth.
Aongstroemia jamaicensis CM.
Campylopus harrisii (CM.) Par.
C. arctocarpus (Hornsch.) Mitt.
Entosthodon bonplandii (Brid.) Mitt.
Hookeriopsis undata (Hedw.) Jaeg.
Hypopterygium tamariscinum (Hedw.) Brid.
Leucobryum antillarum Schp.
L. giganteum CM.
Polytrichum juniperinum Hedw.
Pogonatum robustum Mitt.
Atrichum synoicum (CM.) Par.
Rhizogonium spiniforme (Hedw.) Bruch.
Sphagnum meridense (Hpe.) CM.

On tree trunks or pendant from branches:

Meteoriopsis patula (Hedw.) Broth.
Phyllogonium fulgens (Hedw.) Brid.
Pilotrichella fexilis (Hedw.) Jaeg.
Macromitrium longifolium (Hook.) Brid.
M. punctatum (Hook. & Grey) Brid.
Pirella cavifolia (Card & Herz) Card.
Prionodon densus (Hedw.) CM.

Common genera of hepatics present are:

Anthoceros, Riccia, Pallavicinia, Riccardia, Plagiochila, Dumortiera, Moerchia, Lepidozia, Metzgeria, Marchantia, Trichocollea, Frullania, Calypogeia and *Lejeunea.*

The question of nomenclature for the montane forests of the Caribbean has already received considerable attention. Beard (1942, 1944a) recognised a number of synonyms, preferring "montane rain forest" for the tropics but "temperate rain forest" as a world formation, the formation also occurring in New Zealand, Chile and Formosa. However, in his publication on the vegetation of the Windward and Leeward Isles (1949), he does not mention this term at all but introduces "montane thicket" which, from his description, corresponds to the former "montane rain forest". He also commended the term "cloud forest". Beard does not use the term "montane" as a synonym for "mountain," a wise precaution in the Caribbean where local conditions may bring "montane" formations to low levels.

Barbour (1942) gives details of the nomenclature covering rain forest, cloud forest and so on with equivalents in other languages but does little to clarify the basic concept.

Carabia (1945a) suggests Koppen's climatic system as a possible basis. He considers the term "rain" misleading and suggests "antillean montane forest" as a sub-climax to true rain forest and attempts a broad definition.

The present writers agree that "rain" is misleading. The mist forests of the Caribbean are not controlled by rain but by mist and cloud. The only present solution is to use a suitable term to cover the formation in this region and "montane mist forest" although not ideal, is recommended.

ELFIN WOODLAND

In Jamaica, elfin woodland is found on the exposed summits and northern ridges of the Blue Mountains at 5,000 ft., and over. It is an open woodland of gnarled and twisted trees, often short, windblown and laden with mosses, lichens, ferns and epiphytes. (Fig. 36).

FIG. 36. Elfin woodland on the exposed ridges of the Blue Mountains at 5,000 ft. The pendant moss is *Phyllogonium fulgens.*

The canopy is reduced to 20 ft., the dominants being Clusia and Clethra. Regarded as climax vegetation by Beard (1944a), it is here placed as a faciation of the montane mist forest.

Structure

There is but a single woody stratum; many of the trees which are tall at lower altitudes here mingle with the shrubs. Branching is rambling and distorted, frequently beginning close to ground level. Crowns are sheared and sloping due to wind exposure. Some of the plants have leaves that are fleshy, e.g. Clusia and Hedyosmum, tomentose e.g. Clethra, or small and coriaceous e.g. *Eugenia alpina* and *Ilex obcordata*. The dominant trees are: *Clethra alexandri* and *Clusia havetioides* whilst the following are also conspicuous in the canopy layer: *Vaccinium meridionale, Podocarpus urbanii, Cyrilla racemiflora, Eugenia alpina, Weinmannia pinnata* and *Ilex montana.*

Common shrubs are: *Hedyosmum arborescens, Palicourea crocea, Ilex obcordata, Sciadophyllum browneii* and *Blakea trinerva.*

The field layer contains species from the mist forest including *Pilea parietaria, Peperomia* spp., and *Lycopodium cervicum* is locally present.

Mosses hang in festoons and, with liverworts, form mats on every trunk providing a niche for the small epiphytes, orchids, bromeliads, ferns and lichens.

Elfin woodland is present on the wet limestone slopes of the John Crow Mountains as low as 2,500 ft., and proceeds up to the plateau at 3,500 ft. The latter is worthy of special mention.

Climbing up from the Rio Grande Valley on the western slopes, the attainment of the summit plateau is sudden and definite, so abrupt is the edge of the escarpment. This plateau, tilted eastwards and 2-3 mi. in width, is made up of pinnacled and crevassed limestone simulating the broken surface of glacier ice.

The vegetation is a low, sprawling tangle of mossy trees and shrubs. Every leaf and twig is festooned with dripping bryophytes. Horizontal boughs, sinuous roots and sprawling Clusias lie hidden under a wet verdant mass of epiphytes. The whole is laid, like a tangle of ropes and spars, across the hopeless confusion of large and small fissures and projecting pinnacles of broken limestone. Crevasses and small ravines lie at all angles and are from 6-20 ft. in depth. The only possible progress is across the top of the tangled vegetation where every foothold must be tested before relinquishing the last. Large rock castles up to 20 ft. in height are frequent and each must be circumnavigated. It is small wonder that such an area has been little explored.

The tree layer forms a low but uneven canopy at 15-20 ft., due to the broken topography.

Trees and Shrubs:

Clusia clarendonensis is very abundant, *Clethra occidentalis, Guarea glabra, Eugenia* sp., *Columnea hirsuta, Cyathea gracilis, Psychotria nervosa, Conostegia balbisians, Blakea trinerva, Sciadophyllum brownei, Rheedia sessiliflora, Piper geniculatum.*

Epiphytes include ferns, orchids, bromeliads, herbs and bryophytes:

Begonia glabra, Pilea sp., *Besleria lutea, Lycopodium wilsonii, Cochlidium graminoides, C. seminudum, Polypodium hartii, Rhipidopteris peltata, Trichomanes herbaceum, Diplazium fadyenii, Grammitis trifurcata, Elaphoglossum villosum, Hymenophyllum fucoides,* and *Ctenitis villosa.*

Bryophytes:

Meteoriopsis remotifolia (Hornsch) Broth.
Lepyrodontopsis trichophylla (Sw.) Broth.
Pilotrichum amaonum Mitt.
Rhizogonium spiniforms (Hadw.) Bruch.

On the exposed ridges and peaks of the Blue Mountains, many of the trees of the elfin woodland are stunted and may only reach shrub height forming a low, open forest (Fig. 37). Some of the open places are occupied by thickets of the climbing bamboo *Chusquaea abietefolia* or the ferns *Gleichenia jamaicensis, Odontosoria aculeata, Histiopteris incisa, Paesia viscosa* and *Blechnum lineatum.* In other open areas, the ground is covered with a mat of *Lycopodium clavatum, L. cernuum* or *L. fawcettii.*

FIG. 37. An open aspect of Elfin woodland showing dwarfed Podocarpus and *Clethra alexandrii.* The floor cover is composed of Glychenia and *Lycopodium* sp.

On the exposed north west face of Sir John Peak and Mossmans Peak, the alpine grass *Danthonia shrevei* is found.

Shreve (1914) states that alpine grassland was encountered by Volkens on Kilamanjaro at 7,800 feet only (400 ft. higher than Blue Mountain Peak and 15 degrees lower in latitude). He suggests that, owing to the rapid erosion taking place, Danthonia may be a relict from the comparatively recent times when the Blue Mountains were much higher than the tree limit. The suggestion that such stunted, open woodland represents an approach towards *paramo* or Antillean meadow is tempting. Owing to its very limited expression in Jamaica, however, it is best regarded as an aspect faciation of elfin woodland which may be due to exposure and poor soil development. In some cases, as on Blue Mountain Peak where clearing has taken place in connection with

the erection of triangulation points and huts, such vegetation may well represent a stage of second growth.

SUMMARY AND DISCUSSION

The plant formations and secondary communities recognised in the coastal, lowland and montane regions of Jamaica are shown in Fig. 38. The ecological status and inter-relationship of these communities will now be discussed.

On the coastal sands, an open strand-beach associes of pioneers leads to a closed herbaceous strand dune associes and finally to a climax of Coccoloba-Thespesia, strand woodland. In the vicinity of the southern alluvial plains, the strand sere may be deflected. Here, the stable sand is invaded by cactus-thorn scrub of *Cereus opuntia* and *Acacia tortuosa* which forms a climax community on many of the sand spits. Where raised beaches of coral rock occur, an associes of Tournefortia-Suriana strand scrub is to be found and this leads to a different type of strand woodland in which the palm *Thrinax parviflora* and *Hippomane mancinella* are conspicuous.

In protected coastal areas, where silt is deposited, Mangrove Woodland develops in which the four New World species *Rhizophora mangle, Avicennia nitida, Laguncularia racemosa* and *Conocarpus erecta* are present.

Swamp formations include Mangrove Woodland, Herbaceous Swamp, Palm-Sedge Marsh and Marsh Forest.

Salt flats or salinas frequently fringe the landward margins of Mangrove Woodland in the vicinity of the alluvial plains. They are dominated by an almost exclusive cover of *Batis maritima*. Large salinas show evidence of invasion by adjacent cactus-thorn scrub. These relationships of the coastal communities have been given in Fig. 12.

Freshwater herbaceous swamps are very limited in extent, being confined to low-lying river margins. Typical plants are Typha, Phragmites and *Arundo donax* together with floating and submerged aquatics. Palm-Sedge Marsh and Marsh Forest are confined to the low-lying flood plains of which the Black River produces the most noteworthy example. The former is dominated by *Cyperus* spp. with the sporadic occurrence of the palms *Roystonia princeps* and *Calyptronoma swartzii*. Marsh Forest occurs in slightly higher ground and these two palms together with *Symphonia globulifera* form a closed canopy.

Thorn-scrub dominated by *Prosopis juliflora* is found on the alluvial plains. The ecological conditions necessary for the development of thorn-scrub and its cactus faciation need to be determined before their relationship to one another and to the coastal communities can be fully understood.

The coastal limestone hills support a sub-climax community of Dry Limestone Scrub Forest. This is a relatively open stunted woodland with a great number of species and few large trees. It has been subject to human interference and formerly included a much richer tree flora. This is well shown to-day in

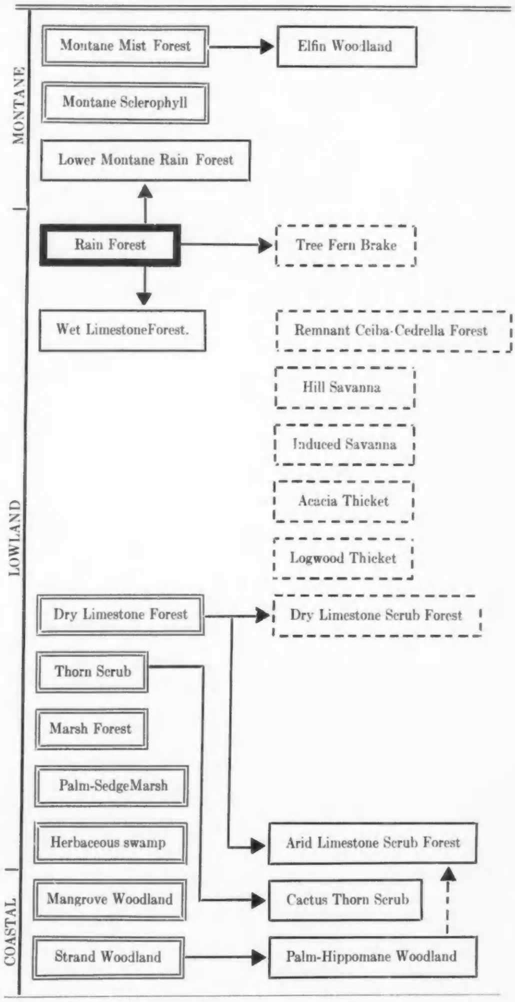
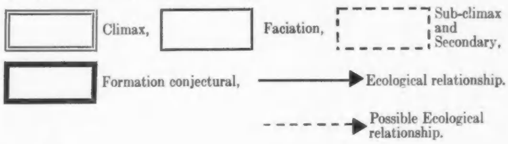


FIG. 38. Scheme to show the Formations and Secondary Communities recognized in Jamaica, their ecological status and inter-relationship.



the Dry Limestone Forest on the ridge at Portland Point where over 80 tree species have been identified forming a canopy at 50-60 ft. and a sub-canopy at 20-30 ft. Arid Limestone Scrub Forest is a coastal faciation of this plant community. Palm-Hippomane Strand Woodland and Arid Limestone Scrub Forest have many species in common which are evergreen and have thick, leathery leaves. The latter community differs mainly in having a larger number of species and these are common to the Dry Limestone Scrub

Forest. We have regarded it as a faciation of Dry Limestone Scrub Forest but it may well be an ecotone between this community and Strand Woodland.

The former presence of forest on the alluvial plains is conjectured from the number of remnant scattered native trees that could form woodland were it not for interference of man and his animals. At the present time, it is replaced by induced savanna, with scattered trees of *Acacia lutea* and *Samanea saman* or by Acacia or logwood thicket.

A remnant forest of large spreading trees including Ceiba and Cedrella occurs in the lower valleys of the shale hills. This was formerly much more widespread on the hills than it is to-day. Shifting cultivation and erosion has led to secondary communities of either induced hill savanna with scattered mango trees or of bamboo brake.

Wet Limestone Forest occurs where the rainfall is over 100 in. per year. It is seen to best advantage at the present time in the elevated Cockpit country. This is a luxuriant evergreen forest which has physiognomic and floristic affinity to Lower Montane Rain Forest. It is considered to be a faciation of Tropical Rain Forest.

No typical Tropical Rain Forest exists in Jamaica to-day but, from the Tree Fern Brake of the Rio Grande Valley, its former presence is a very reasonable conjecture. Tree Fern Brake is regarded as a secondary or sub-climax community to Rain Forest. It does not occur at the present time outside the Rio Grande Valley. Ørsted, who spent six weeks in Jamaica in 1846, made the tree-ferns of Jamaica classical. He wrote "There is probably no other place on earth where the tree-ferns attain such considerable height and where, furthermore, these ferns form such large continuous woods displacing all other plants, as can be found in the Jamaican mountains." He is taken to task rather sharply over these remarks by Brockman-Jerosch who visited Jamaica in 1914 but failed to see tree-fern brake. However, Ørsted's map (Fig. 39) is highly informative. He supports his description by sketching in a wide belt of tree-fern brake below the mist forest on the northern slopes of the Blue Mountains. This is clearly the result of clearing which is also indicated. Man and not the tree-ferns have "displaced" the other plants. It is to be noted that the tree-fern brake is shown for the north slopes where it has apparently followed clearing of lower montane rain forest.

Lower Montane Rain Forest is still to be found in the less accessible wet northern slopes of the Blue Mountains and the western slopes of the John Crow Mountains bounding the Rio Grande Valley. It is a montane faciation of lowland Tropical Rain Forest. Two types have been observed. One is a mixed forest dominated by tall, straight boled trees such as *Psidium montanum*, *Calophyllum jacquinii*, *Matayba apetala* and *Symphonia globulifera*. In the other type, *Calophyllum jacquinii* alone is dominant.

Montane Sclerophyll is typical of the dry, southern slopes of the Blue Mountains between altitudes of 2,500-4,000 ft. It has two aspects—a lower, open

FIG. 39. Vegetation of Jamaica (From A. S. Ørsted. Courtesy of Arnold Arboretum of Harvard University). Note the coastal vegetation, the dry southern plains and the upland plateau of Manchester, with scattered bottle-shaped cotton trees, rising to the wet cockpit areas. The north-eastern aspect is shown on the right and includes the Lowland Tropical Rain Forest of the Rio Grande valley with the John Crow Mountains on the left. The lower slopes of the Blue Mountains already show coffee plantations, patchwork cultivation and second growth tree fern brake. The higher reaches support Mist Forest.

zone consisting of xerophytic shrubs widely dispersed in a ground flora of grasses. Shifting cultivation prevails and burning here prevents the spread of the shrubs but encourages the spread of the introduced grass *Melinis minutiflorus* and the fern *Gleichenia pectinata*. These plants are rapidly dominating large areas. Above this zone is a less disturbed and more closed sclerophyllous thicket of dwarf, spindly trees and shrubs in which *Cyrilla racemiflora, Clethra occidentale* and *Vaccinium meridionale* are conspicuous. The lower bushy sclerophyll zone is thought to be a secondary developmental community which, if undisturbed, would lead to sclerophyllous thicket in these seasonally dry areas. There is, however, some indication that, where it occurs in wetter regions, it may bear the same relationship to Lower Montane Rain Forest.

Montane Mist Forest occurs extensively in the Blue Mountain range above 4,500 ft. It is shrouded in mist for most of the day. Low-canopied evergreen trees are associated with an abundance of undershrubs, ferns, bryophytes and lichens. Elfin Woodland which occurs on the exposed ridges and summits, is regarded as an open faciation of the Mist Forest. Fig. 40 shows the distribution of some of the vegetation units as seen in a diagrammatic cross section of the island from the Parish of Portland in the north-east running south-west to the Parish of St. Andrew.

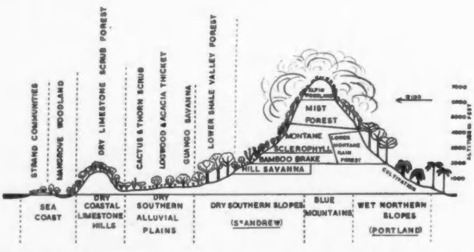


FIG. 40. Diagrammatic representation of the vegetation seen in a cross section of the eastern end of the island passing through the parishes of Portland and St. Andrew.

It will be profitable to relate the vegetation as a whole with the Formations proposed by Beard (1944a) for use throughout Tropical America and the Caribbean. Beard follows the present trend in tropical ecology and recognises physiognomic units, as distinct from floristic units, each with a characteristic essential habitat. He distinguishes an optimal Formation "where every condition for plant growth is as ideally favourable as it can be in the tropics" and Formation Series "within which are structures and life forms expressing every degree of transition from the optimum to extreme adversity." The optimal Formation type is Rain Forest. The Formation Series, each of which is based on a major type of habitat, are as follows:

i. Seasonal Formations
ii. Dry Evergreen Formations
iii. Montane Formations
iv. Swamp Formations
v. Marsh (Seasonal Swamp) Formations

The swamp and marsh formations may be considered to be edaphic climax formations—the remainder, including the optimal Formations are climatic climax formations. Within each Formation Series are units arranged in regard to moisture relations but distinguished purely on physiognomic data. In the Seasonal Formations, for example, where the characteristic of the habitat is seasonal drought, there is Evergreen Seasonal Forest ranging through Deciduous Seasonal Forest to Scrub and finally Desert.

With time and practical application, Beard has seen fit to modify and make additions to his system for which reference should be made to his publications. The Pan-Caribbean Forestry Meeting in 1946 adopted Beard's system until "further work should confirm or decry its utility." The following discussion is a contribution towards that end.

In Table 6 may be seen the correlation of the major vegetation types recognised in Jamaica by the authors with the Formations proposed by Beard.

TABLE 6. The Vegetation of Jamaica in relation to the Caribbean Climax Formations of Beard (1944a).

Main Vegetation Types Recognized in Jamaica	Equivalent Vegetation Types Recognized by Beard
Conjectured from presence of Tree Fern Brake	1. OPTIMAL FORMATION Rain Forest
	2. SEASONAL FORMATIONS
Wet Limestone Forest?	Evergreen Seasonal Forest
Dry Limestone Scrub Forest	Semi-Evergreen Seasonal Forest?
Thorn Scrub	Thorn Woodland
Cactus-Thorn Scrub	Cactus Scrub
	3. DRY EVERGREEN FORMATIONS
Strand Woodland	Littoral Woodland
	4. MONTANE FORMATIONS
Lower Montane Rain Forest	Lower Montane Rain Forest
Montane Mist Forest	Montane Rain Forest
Palm Brake?	Palm Brake
Elfin Woodland	Elfin Woodland
Montane Sclerophyll	No equivalent
	5. SWAMP FORMATIONS
Herbaceous Swamp	Herbaceous Swamp
Mangrove Woodland	Mangrove Woodland
	6. MARSH (SEASONAL SWAMP) FORMATION
Marsh Forest	Marsh Forest
Palm-Sedge Marsh	Palm Marsh

The Optimal Formation type, i.e. Tropical Rain Forest, as defined by Beard, permits of no physiognomic variation since the habitat conditions are uniformly favourable all the year round. This is, perhaps, too rigid a definition. It is felt that both Evergreen Seasonal Forest, with which our Wet Limestone Forest corresponds in structure and seasonal moisture relations, and Lower Montane Rain

Forest might well be regarded as faciations of typical Rain Forest.

Although the Dry Limestone Forests undoubtedly belong to the Seasonal Formation Series, more details of their physiognomy are required before they can be correlated with certainty. At the moment, all that can be said is that there would seem to be a greater affinity to Semi-Evergreen Seasonal Forest than Deciduous Seasonal Forest although the severe habitat conditions would lead one to expect the latter formation type. No doubt, in former times, there were present in Jamaica more luxuriant gradations of this type of seasonal forest in areas of decreasing seasonal drought, which culminated in Wet Limestone Forest. Such areas are now mainly under cultivation and pasture. The remnants that are left have not yet been studied.

Cactus-thorn Scrub is considered by the authors to be a faciation of Thorn Scrub.

The habitat conditions for the Dry Evergreen Formations as defined by Beard are well-drained lands where the moisture supply is not seasonal but fairly consistently inadequate all the year round. This may be due to strong winds and excessively porous soil. The typical species are hard-leaved evergreens. Strand Woodland corresponding to Beard's Littoral Woodland is a member of this formation series.

In Jamaica, there is a seasonal drought in all low-lying coastal areas, with the possible exception of the northeast, which is just as severe as that prevailing on the coastal limestone hills supporting deciduous seasonal forest. Yet there is this abrupt change to small, hard-leaved, evergreen woodland. It is suggested that here it is the presence of salt laden winds that are responsible rather than consistent drought. The fact that the coastal faciation of dry limestone forest has many evergreen species in common with strand woodland is significant in this respect.

Montane Mist Forest corresponds to Beard's Montane Rain Forest. Daily mist is the most notable characteristic of the habitat and the authors suggest that Mist Forest is the better term. Elfin Woodland is regarded as an open stunted faciation of Mist Forest, brought about by more exposed conditions, since, for the most part, it is made up of species common in the Mist Forest. Montane Sclerophyll has no counterpart in Beard's classification. Later he uses the term "Montane Thicket" which might well be a suitable one for the upper sclerophyllous thicket of Jamaica, but, from his description of this community, it would seem to be a synonym for his Montane Rain Forest. A community that would seem to correspond to Palm Brake occurs in the western slopes of the John Crow Mountains above Lower Montane Rain Forest. It has not yet been investigated. The swamp and marsh communities of Jamaica fit in very well with Beard's nomenclature and need no further comment.

In conclusion, it may be said that Beard's classification as applied to Jamaica, receives general ratification. Whether it is desirable to separate Evergreen Seasonal Forest and Lower Montane Rain Forest so markedly from Tropical Rain Forest is doubtful. It is suggested that the controlling habitat factor for Littoral Woodland is the presence of salt-laden winds, not consistent drought. A type of seasonal forest called Dry Limestone Scrub Forest is produced in Jamaica under the latter conditions. The addition of Montane Sclerophyll to the Montane Formation series is desirable.

The present vegetation of Jamaica enables reasonably accurate reconstruction of the original vegetation of the island to be made. Early descriptions of dense jungles with the impression of extensive lowland tropical rain forest must be discounted.

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APPENDIX

The nomenclature adopted by Fawcett & Rendle has been followed wherever possible. For plants not covered by this Flora, reference has been made to the Jamaica Herbarium and the following works:

Flora of the British West Indian Islands by A. H. R. Grisebach (1864); The Botany of Porto Rico and the Virgin Islands by N. L. Britton (1923-26); Flora de Cuba by Leon (1946) and Leon & Alain (1951); Manual of the grasses of the West Indies by A. S. Hitchcock (1936); A preliminary check-list of Jamaican pteridophytes by G. R. Proctor (1953).

The mosses have been checked by E. Bartram, and the marine algae by Prof. V. J. Chapman. They are not included in the appendix since authorities are given in the text.

A check-list of plants mentioned in the text (excluding the bryophytes and marine algae) follows.

Dicotyledons

Acanthaceae

Andrographis paniculata Ns.
Barleria prionitis L.
Blechum brownei Juss.
Pachystachys coccinea Ns.
Ruellia tuberosa L.
Thunbergia fragrans Roxb.

Amarantaceae

Achyranthes indica Mill.
Alternanthera ficoidea Roem. & Schult.
A. parvifolia Fawc. & Rendle
A. repens Kuntze.
Amarantus viridus L.
A. spinosus L.
Celosia argentea L.
Gomphrena globosa L.
Iresine paniculata Kuntze
Philoxerus vermicularis Beauv.

Anacardiaceae

Anacardium occidentale L.
Comocladia pinnatifolia L.
C. velutina Britton
Mangifera indica L.
Mosquitoxylon jamaicense Kr. & Urb.
Rhus metopium L.
Spondias monbin L.
S. purpurea L.

Anonaceae

Anona glabra L.
A. palustris L.
A. reticulata L.
A. squamosa L.
Oxandra lanceolata Braill.
Oxandra laurifolia A. Rich.
Xylopia muricata L.

Apocynaceae

Echites suberecta Jacq.
E. umbellata Jacq.
Plumeria alba L.

Aquifoliaceae

Ilex montana Griseb.
I. obcordata Sw.

Araliaceae

Gilibertia arborea March.
G. nutans March.
G. ovalifolia Fawc. & Rendle
Sciadophyllum brownei Spreng.

Aristolochiaceae

Aristolochia odoratissima L.
A. trilobata L.

Asclepiadaceae

Asclepias curassavica
A. nivea L.
Metastelma atrorubens Schlecht.
M. fawcettii Schlecht.
M. harrisii Schlecht.

Balanophoraceae

Scybalium jamaicense Schott & Endl.

Batidaceae

Batis maritima L.

Begoniaceae

Begonia acutifolia Sw.
B. glabra Aubl.

Bignoniaceae

Catalpa longissima Sims.
Cresentia cujete L.
Schlegelia parasitica Mrs.
Spathodea campanulata Beauv.
Tecoma leucoxylon Mart.
T. stans Juss.

Bombacaceae

Ceiba pentandra Gaertn.
Ochroma pyramidale Urb.

Boraginaceae

Beureria succulenta Jacq.
Cordia alba R. & Sch.
C. collococca L.
C. cylindristachya R. Sch.
C. gerascanthoides H. B. K.
C. nitida Vahl
C. sebestana Jacq.
Heliotropium curassavicum L.
H. parviflorum L.
Tournefortia astrotrichia DC.
T. cymosa (L.) DC.
T. gnaphalodes R. Br.
T. hirsutissima L.
T. volubilis L.

Brunelliaceae

Brunellia comocladifolia Humb. & Bonpl.

Burseraceae

Bursera simaruba Sarg.
B. simplicifolia DC.

Cactaceae

Cereus flagelliformis Miller
C. peruvianus Miller
C. triangularis Haw.
Melocactus communis Link & Otto
Opuntia jamaicensis Britt. & Harris
O. spinosissima Miller
O. tuna Miller

Caesalpiniaceae

Bauhinia divaricata L.
Caesalpinia bonducella Fleming
C. coriaria Willd.
C. vesicaria L.
Cassia emarginata L.
C. viminea L.
Haematoxylon campechianum L.
Hymenaea courbaril L.
Parkinsonia aculeata L.
Peltophorum brasiliense Urb.
Poinciana regia Boj.
Tamarindus indica L.

Campanulaceae

Lobelia acuminata Sw.
L. assurgens L.

Canellaceae

Canella winterana Gaertn.
Cinnamodendron corticosum Miers.

Capparidaceae

Capparis cynophallophora L.
C. ferruginea L.
C. flexuosa L.
Cleome serrata Jacq.
C. spinosa Jacq.
Crataeva gynandra L.
C. tapia L.

Caprifoliaceae

Viburnum villosum Sw.

Caricaceae

Carica jamaicensis Urb.

Casuarinaceae

Casuarina equisetifolia Forst.

Celastraceae

Gyminda latifolia Urb.
Rhacoma crossopetalum L.
Schaefferia frutescens Jacq.

Ceratophyllaceae

Ceratophyllum demersum L.

Chenopodiaceae

Atriplex cristata Humb. & Bonpl.
Salicornia ambigua Michx.

Chloranthaceae

Hedosymum arborescens Sw.
H. nutans Sw.

Clethraceae

Clethra alexandri Griseb.
C. occidentalis (L.) Steud.

Combretaceae

Bucida buceras L.
Buchenavia capitata Eichl.
Conocarpus erecta L.
Laguncularia racemosa Gaertn.
Terminalia catappa L.
T. latifolia Sw.

Compositae

Ambrosia hispida Pursh
Baccharis scoparia (L.) Sw.
Bidens cynapiifolia H. B. K.
B. pilosa L.
B. reptans (L.) G. Don.
Borrichia arborescens (L.) DC.
Egletes prostrata (Sw.) Kuntze
Erigeron canadensis L.
Eupatorium dalea L.
E. odoratum L.
Gnaphalium americanum Mill.
Isocarpha oppositifolia (L.) R. Br.
Pectis ciliaris L.
P. febrifuga van Hall
Senecio discolor (Sw.) DC.
Sonchus oleraceus L.
Spilanthes urens Jacq.
Verbesina pinnatifida Sw.
Vernonia divaricata Sw.

Connaraceae

Rourea paucifoliolata Planch.

Convolvulaceae

Calonyction tuba Schlecht.
Cuscuta americana L.
Ipomea carnea Jacq.
I. fastigiata Swt.
I. jamaicensis G. Don.
I. pes-caprae Sw.
I. quinquefolia L.
I. sidifolia Choisy.
I. umbellata Mey.

Crassulaceae

Bryophyllum pinnatum Kurz.

Cruciferae

Cakile lanceolata O. E. Schulz.

Cucurbitaceae

Cionosicys pomiformis Griseb.
Cucumis anguria L.
Momordica charantia L.

Cunoniaceae

Weinmannia pinnata L.

Cyrillaceae

Cyrilla racemiflora L.

Ebenaceae

Diospyros tetrasperma Sw.

Ericaceae

Lyonia jamaicensis Don

Erythroxylaceae

Erythroxylon areolatum L.
E. rotundifolium Lun.

Euphorbiaceae

Acalypha scabrosa Sw.
A. virgata L.
Acidoton urens Sw.
Adelia ricinella L.
Alchornea latifolia Sw.
Argythamnia candicans Sw.
Bernardia carpinifolia Griseb.
Croton flavens L.
C. glabellus L.
C. grisebachianus Muell.
C. humilis L.
C. linearis Jacq.
C. ovalifolius Vahl.
Drypetes lateriflora Kr. & Urb.
Euphorbia buxifolia Lam.
E. blodgettii Engelm.
E. heterophylla L.
E. hirta L.
E. hypericifolia L.
Gymnanthes elliptica Sw.
G. lucida Sw.
Hippomane mancinella L.
Hura crepitans L.
Jatropha gossypifolia L.
Lasiocroton macrophyllus Griseb.
Phyllanthus acuminatus Vahl
P. angustifolius Sw.
P. epiphyllanthus L.
P. linearis Sw.
P. niruri L.
Picrodendron baccatum Kr. & Urb.
Ricinus communis L.
Sapium jamaicense Sw.
Securinega acidoton Fawc. & Rendle
Tragia volubilis L.

Ficoideaceae

Sesuvium portulacastrum L.

Flacourtiaceae

Casearia guianensis Urb.
C. hirsuta Sw.
C. nitida Jacq.
Laetia thamnia L.

Garryaceae

Garrya fadyenii Hook.

Gentianaceae

Eustoma exaltatum Griseb.
Leianthus longifolius Griseb.

Gesneriaceae

Achimenes coccinea Pers.
Besleria lutea L.
Columnea hirsuta Sw.
Rytidophyllum grande Mart.

Goodeniaceae

Scaevola plumierii (L.) Vahl

Guttiferae

Calophyllum jacquinii Fawc. & Rendle
Clusia clarendonensis Britton
C. flava Jacq.
C. havetioides Planch.
C. rosea Jacq.
Mammea americana L.
Rheedia pendula Urb.
R. sessiliflora Planch.
Symphonia globulifera L. f.

Hernandiaceae

Hernandia catalpifolia Britt. & Harris

Hypericaceae

Ascyrum hypericoides L.

Labiatae

Hyptis capitata Jacq.
Leonurus sibiricus L.
Micromeria obovata Benth.
Salvia occidentalis Sw.

Lacistemaceae

Lacistema aggregatum Fawc. & Rendle

Lauraceae

Hufelandia pendula Nees
Misanteca triandra Mez.
Nectandra antillana Meisn.
N. coriacea Griseb.
N. patens Griseb.
N. sanguinea Roland ex. Rottb.
Ocotea jamaicensis Mez.
O. martinicensis Mez.
O. staminea Mez.
Persea alpigena Spreng.

Lentibulariaceae

Utricularia stellaris L.

Loganiaceae

Spigelia anthelmia L.

Malpighiaceae

Byrsonima coriacea DC.
Heteropteris laurifolia A. Juss.
Malpighia glabra L.
M. punicifolia L.
Stigmaphyllon emarginatum A. Juss.

Malvaceae

Abutilon giganteum Sweet.
Hibiscus elatus Sw.
Pavonia rosea Schlecht.
Sida procumbens Sw.
S. rhombifolia L.
Thespesia populnea Solander

Marcgraviaceae

Marcgravia brownei Kr. & Urb.

Melastomaceae

Blakea trinervia L.
Conostegia balbisiana Ser.
C. superba Naud.
Heterotrichum umbellatum Urb.
Mecranium amygdalinum Triana.
M. purpurascens Triana.
M. virgatum Triana.
Meriania leucantha Sw.
M. purpurea Sw.
Miconia dodecandra Cogn.

M. laevigata DC.
M. quadrangularis Naud.
M. rubens Naud.
Ossaea asperifolia Triana.

Meliaceae

Cedrela odorata L.
Guarea glabra Vahl
Swietenia mahogani Jacq.
Trichilia hirta L.

Menispermaceae

Cissampelos pareira L.
Hyperbaena domingensis Benth.

Mimosaceae

Acacia lutea Hitchc.
A. tortuosa Willd.
A. villosa Willd.
Adenanthera pavonina L.
Albizzia lebbeck Benth.
A. berteriana (Balbis) Maza.
Enterolobium mangense Fawc. & Rendle
E. saman Prain.
Inga vera Willd.
Leucaena glauca Benth.
Mimosa pudica L.
Pithecellobium alexandri Urb.
P. arboreum Urb.
P. unguis-cati Benth.
P. dulce Benth.
Prosopis juliflora DC.

Moraceae

Artocarpus incisa L.
Artocarpus integrifolia L.
Brosimum alicastrum Sw.
Cecropia peltata L.
Chlorophora tinctoria Gaudich.
Ficus aurea Nutt.
F. harrisii Warb.
F. mamillifera Warb.
F. morantensis Britton
F. populnea Willd.
F. suffocans Griseb.
F. wilsonii Warb.
Trophis racemosa Urb.

Moringaceae

Moringa oleifera Lam.

Myricaceae

Myrica microcarpa Benth.

Myrsineae

Rapanea ferruginea R. & P.

Myrtaceae

Calyptranthes chytraculia Sw.
Calyptranthes pallens Griseb.
Eugenia alpina Willd.
E. axillaris Willd.
E. biflora DC.
E. buxifolia Willd.
E. disticha DC.
E. fragrans Willd.
E. jambos L.
E. malaccensis L.
E. marchiana Griseb.
E. monticola DC.
E. rhombea Kr. & Urb.
Pimenta officinalis Lindl.
Psidium albescens Urb.
P. guajava L.
P. montanum Sw.

Nyctaginaceae

Boerhavia scandens L.
Mirabilis jalapa L.
Pisonia aculeata L.
P. fragrans Dumont.
P. obtusata Jacq.

Nymphaeaceae

Nymphaea alba L.

Oleaceae

Linociera ligustrina Sw.
Ximenia americana L.

Onagraceae

Jussiaea suffruticosa L.

Papaveraceae

Argemone mexicana L.
Bocconia frutescens L.

Papilionaceae

Abrus precatorius L.
Andira inermis H. B. K.
Brya ebenus DC.
Canavalia obtusifolia DC.
Centrosema virginianum Benth.
Crotalaria retusa L.
C. verrucosa L.
Dalbergia brownei Urb.
D. ecastaphyllum Taub.
Desmodium supinum DC.
Flemingia strobilifera R. Br.
Galactia pendula Pers.
Gliricidia sepium Steud.
Indigofera tinctoria L.
Lonchocarpus latifolius H. B. K.
Mucuna pruriens DC.
Piscidia piscipula Sarg.
Pterocarpus officinalis Jacq.
Sophora tomentosa L.

Passifloraceae

Passiflora penduliflora Bertero.
P. perfoliata L.
P. rubra L.
P. suberosa L.

Phytolaccaceae

Petiveria alliacea L.
Rivina humilis L.

Piperaceae

Piper aduncum L.
P. amalago L.
P. arboreum Aubl.
P. discolor Sw.
P. geniculatum C. DC.
P. hispidum Sw.
P. nigrinodum C. DC.
P. otophyllum C. DC.
P. scabrum Sw.
Peperomia amplexicaulis A. Dietr.
P. cordifolia A. Dietr.
P. crassicaulis Fawc. & Rendle
P. hispidula A. Dietr.
P. verticillata A. Dietr.

Plumbaginaceae

Plumbago scandens L.

Polygonaceae

Antigon leptopus Hook.
Coccoloba diversifolia Jacq.
C. krugii Lindau.
C. laurifolia Jacq.
C. littoralis Urb.
C. longifolia Fisch.
C. uvifera L.

Portulacaceae

Portulaca oleracea L.
Talinum paniculatum Gaertn.

Quiinaceae

Quiinia jamaicensis Griseb.

Ranunculaceae

Clematis dioica L.

Rhamnaceae

Colubrina asiatica Brongn.
C. ferruginosa Brongn.
C. reclinata Brongn.
Gouania lupuloides Urb.
Krugiodendron ferreum Urb.
Rhamnus sphaerosperma Sw.
Rhamnidium jamaicense Urb.
Sarcomphalus laurinus Griseb.
Zizyphus chloroxylon Oliv.
Z. jujuba Lam.

Rhizophoraceae

Cassipourea elliptica Poir.
Rhizophora mangle L.

Rosaceae

Chrysobalanus icaco L.
Prunus myrtifolia Urb.
P. occidentalis Sw.

Rubiaceae

Antirrhoea jamaicensis (Griseb.) Urb.
Borreria laevis (Lam.) Griseb.
Catesbaea parviflora Sw.
Cephaelis elata Sw.
Chiococca alba (L.) Hitchc.
Coccocypselum herbaceum Aubl.
Erithalis fruticosa L.
Ernodea littoralis Sw.
Exostema caribaeum (Jacq.) Roem. & Schult.
Faramea occidentalis (Jacq.) A. Rich.
Guettarda argentea Lam.
G. elliptica Sw.
G. longiflora Griseb.
Machaonia rotundata Griseb.
Manettia lygistum (L.) Sw.
Morinda citrifolia L.
M. royoc L.
Palicourea crocea (Sw.) Roem. & Schult.
Portlandia grandiflora L.
P. latifolia Britt. & Harris.
Psychotria balbisiana DC.
P. brachiata Sw.
P. browneii Spreng.
P. corymbosa Sw.
P. nervosa Sw.
P. pedunculata Sw.
Randia aculeata L.
Relbunium hypocarpium (L.) Hemsl.
Rondeletia hirta Sw.
R. tomentosa Sw.

R. trifolia Jacq.
Schradera involucrata (Sw.) K. Schum

Rutaceae

Amyris balsamifera L.
Amyris elemifera L.
Esenbeckia pentaphylla Griseb.
Spathelia glabrescens Planch.
Spathelia sorbifolia L.
Zanthoxylum fagara Sarg.
Zanthoxylum flavum Vahl
Zanthoxylum martinicense DC.
Zanthoxylum spinosum Sw.

Sapindaceae

Allophylus cominia Sw.
A. jamaicensis Radlk.
A. pachyphyllus Radlk.
Cardiospermum grandiflorum Sw.
Dodonaea viscosa Jacq.
Exothea paniculata Radlk.
Hypelate trifoliata Sw.
Matayba apetala Radlk.
Melicocca bijuga L.
Paullinia barbadensis Jacq.
Sapindus saponaria L.
Serjania laevigata Radlk.

Sapotaceae

Achras sapota L. (=*Sapota sideroxylon* Griseb.)
Bumelia retusa Sw.
B. rotundifolia Sw.
Chrysophyllum cainito L.
C. oliviforme Lam.
Dipholis montana Griseb.
D. nigra Griseb.
D. salicifolia A. DC.
Lucuma mammosa Gaertn.
Mimusops excisa Urb.
Sideroxylon foetidissimum Jacq.

Scrophulariaceae

Maurandia erubescens (Don) A. Gray

Simarubaceae

Castela macrophylla Urb.
Picraena excelsa Lindl.
Picramnia antidesma Sw.
Simaruba glauca DC.
Suriana maritima L.

Solanaceae

Acnistus arborescens Schlecht.
Capsicum frutescens L.
Cestrum diurnum L.
C. hirtum Sw.
Datura stramonium L.
D. suaveolens Humb. & Bonpl.
Solandra grandiflora Sw.
Solanum havanense Jacq.
S. punctulatum Dun.
S. torvum Sw.
S. verbascifolium L.

Staphylaceae

Turpinia occidentalis G. Don

Sterculiaceae

Ayenia laevigata Sw.
Cola acuminata Schott & Endl.
Guazuma ulmifolia Lam.
Helicteres jamaicensis Jacq.
Melochia crenata Vahl
M. lupulina Sw.
M. tormentosa L.
Theobroma cacao L.
Waltheria americana L.

Ternstroemiaceae

Eroteum theoides Sw.
Laplacea haematoxylon G. Don.

Thymelaeaceae

Daphnopsis occidentalis Kr. & Urb.
Lagetta lagetto Nash

Tiliaceae

Corchorus siliquosus L.
Sloanea jamaicensis Hook.

Turneraceae

Turnera ulmifolia L.

Ulmaceae

Celtis trinervia Lam.
Trema micrantha Bl.

Umbelliferae

Hydrocotyle umbellata L.

Urticaceae

Boehmeria caudata Sw.
B. jamaicensis Urb.
Gyrotaenia microcarpa Fawc. & Rendle
G. spicata Wedd.
Pilea ciliata Blume
P. crassifolia Blume
P. reticulata Wedd.
P. microphylla Liebm.
P. parietaria Griseb.

Vacciniaceae

Vaccinium meridionale Sw.

Verbenaceae

Aegiphila elata Sw.
Avicennia nitida Jacq.
Citharexylum caudatum L.
C. fruticosum L.
Duranta plumieri Jacq.
Lantana crocea Jacq.
L. involucrata L.
Lippia reptans H. B. K.
Priva echinata Juss.
Stachytarpheta indica Vahl
Vitex umbrosa Sw.

Vitaceae

Cissus cucurbitacea Britt.
C. sicyoides L.

Zygophyllaceae

Guaicum officinale L.
Tribulus cistoides L.

MONOCOTYLEDONS

Amaryllidaceae

Agave americana L.
Hymenocallis speciosa Salisb.

Araceae

Philodendron spp.
Pistia stratiotes L.

Bromeliaceae

Aechmea paniculigera Griseb.
Bromelia pinguin L.
Hohenbergia distans Griseb.
H. erythrostachya Brongn.
Thecophyllum sintenisii (Baker) Mez.
Tillandsia balbisiana Schult.
T. incurva Griseb.
T. recurvata L.
T. usneoides L.

Cyperaceae

Cyperus brunneus Sw.
C. giganteus Vahl
C. retundus L.
Fimbristylis ferruginea (L.) Vahl
Mariscus jamaicensis Britton
Rhynchospora eggersiana Boekl.
Uncinia hamata (Sw.) Urb.

Dioscoraceae

Dioscorea polygonoides H. & B.
Rajania caudata L.

Gramineae

Andropogon pertusus (L.) Willd.
A. virginicus L.
Arundo donax L.
Cenchrus pauciflorus Benth.
C. tribuloides L.
C. echinatus L.
Chloris petraea Swartz
Chusquea abietifolia Griseb.
Cynodon dactylon (L.) Pers.
Danthonia schrevei Britton
Eragrostis ciliaris (L.) Link
Lasiacis divaricata (L.) Hitchc.
Manisuris altissima (Poir) Hitchc.
Melinis minutiflora Beauv.
Panicum maximum Jacq.
P. palmifolium Willd.
P. purpurascens Raddi.
Paspalum fimbriatum H. B. K.
P. saccharoides Nees
P. vaginatm Swartz
Phragmites communis Trin.
Spartina patens var. *juncea* H. Hitchc.
Sporobolus indicus (L.) R. Br.
S. virginicus (L.) Kunth
Uniola virgata (Poir) Griseb.

Hydrocharidaceae

Thalassia testudinum Konig.

Lemnaceae

Lemna minor L.

Liliaceae

Smilax balbisiana Kunth.
S. domingensis Willd.

Musaceae

Heliconia caribaea Lam.

Orchidaceae

Bletia purpurea (Lam.) DC.
Broughtonia sanguinea (Sw.) R. Br.
Dichaea glauca Lindl.
D. graminea Griseb.
Elleanthus capitatus Rchb.
Epidendrum fragrans Sw.
E. verrucosum Sw.
Lepanthes concinna Sw.
L. concolor Fawc. & Rendle
L. tridentata Sw.
Liparis elata Lindl.
Stelis ophioglossoides Sw.

Palmaceae

Acrocomia aculeata (Jacq.) Lodd.
Calyptronoma swartzii Griseb.
Coccothrinax fragrans Burret.
Cocos nucifera L.
Roystonea princeps (Becc.) Burret.
Sabal jamaicensis Becc.
Thrinax excelsa Lodd.
T. parviflora Sw.
T. tesselata Becc.

Pontederiaceae

Eichhornia crassipes Solms.

Potamogetonaceae

Cymodocea manatorum Aschers

Typhaceae

Typha angustifolia L.

GYMNOSPERMAE

Pinaceae

Juniperus barbadensis L.

Taxaceae

Podocarpus purdieanus Hook.
P. urbani Pilger (*P. coriaceus* Rich.)

PTERIDOPHYTA

Acrostichum aureum L.
Adiantum melanoleucum Willd.
A. tenerum Sw.
Alsophila aspera R. Br. (*Cyathea aspera* Sw.)
A. swartziana Mart. (*C. armata* Sw.)
Anemia hirsuta (L.) Sw.
A. underwoodiana Maxon
A. adiantifolia (L.) Sw.
Asplenium alatum Humb. & Bonpl.
A. cuneatum Lam.
A. harpeodes Kunze
A. praemorsum Sw.
A. pumilum Sw.
A. radicans L.
Azolla carolinana Willd.
Blechnum jamaicense (Broadh.) C. Chr.
B. lineatum (Sw.) C. Chr.
B. polypodioides (Sw.) Kuhn
B. unilaterale Sw.
Bolbitis aliena (Sw.) Alston
B. nicotianaefolia (Sw.) Alston
B. pergamentacea (Maxon) Ching.
Camptodium pedatum (Desv.) Fee
Campyloneuron angustifolium (syn. *Polypodium angustifolium* Sw.)
Cheilanthes microphylla Sw.
C. trichomanoides (L.) Mett.
Cochlidium graminoides (Sw.) Kaulf (*C. seminudatum* (Willd.) Maxon)
Ctenitis ampla (H. B. W.) Copel.
C. effusa (Sw.) Copel.
Ctensis villosa (L.) Copel.
Cyathea armata (Sw.) Domin.
C. aspera (L.) Sw.
C. gracilis Griseb.
C. tussacii Desv.
C. nigrescens (Hook) J. Sm.
C. pubescens Mett. ex. Kuhn.
C. grevilleana Mart.
Cystopteris fragilis (L.) Bernh.
Danaea jamaicensis Underw.
D. jenmani Underw.
D. nodosa (L.) J. E. Smith.
Dennstaedtia bipinnata (Cav.) Maxon
D. cicutaria (Sw.) Moore
D. globulifera (Poir) Hieron
Diplazium brunneo-viride (Jenm.) C. Chr.
D. centripetale (Baker) Maxon
D. costale (Sw.) Presl
D. fadyeni (Hook) Proctor
D. pectinatum (Fee) C. Chr.
Doryopteris pedata (L.) Fee
Dryopteris decussata (syn. *Thelypteris decussata* (L.) Proctor)
D. deltoidea (syn. *Thelypteris deltoidea* (Sw.) Proctor)
D. denticulata (Sw.) Ktze.
D. gemmipara (C. Chr.) Maxon
D. heteroclita (syn. *Thelypteris heteroclita* (Desv.) Proctor)
Dryopteris resinifera (syn. *Thelypteris resinifera* (Desv.) Proctor)
Elaphoglossum eggersii (Baker) Christ.
E. petiolatum (Sw.) Urban
E. simplex (Sw.) Schott.
E. villosum (Sw.) J. Sm.
Gleichenia jamaicensis (Underw.) Proctor
G. pectinata (Willd.) Presl
Grammitis hartii (Jenm.) Proctor
G. serrulata (Sw.) Sw.
G. trifurcata (L.) Copel.
Gymnopteris rufa (L.) Bernh.
Histiopteris incisa (Thunb.) J. Sm.
Hymenophyllum fucoides Sw.
H. hirsutum (L.) Sw.
H. hirtellum Sw.
H. lanatum Fee
H. polyanthos (Sw.) Sw.
H. sericeum (Sw.) Sw.
Lomariopsis underwoodii Holttum
Lophosoria quadripinnata (Gmel) C. Chr.
Lycopodium cernuum L.
L. fawcettii Lloyd & Underw.
L. wilsoni Underw. & Lloyd
L. clavatum L.
Lygodium volubile Sw.
Marattia alata Sw.
Nephrolepis pectinata (Willd.) Shott.
N. rivularis (Vahl) Mett.
Notholaena trichomanoides (syn. *Cheilanthes trichomanoides* (L.) Mett.)
Orthiopteris domingensis Spreng.
Paesia viscosa St. Hil.
Polybotrya cervina (L.) Kaulf.
Polypodium angustifolium Sw.
P. dissimile L.
P. exornans Maxon
P. hartii (syn. *Grammitis hartii* (Jenm.) Proctor)
P. heterophyllum L.
P. jubaeforme Kaulf.
P. loriceum L.
P. lycopodioides L.
P. mollissimum Fee
P. thyssanolepis A. Br. ex. Klotzsch.
Polystichum christianae (Jenm.) Udderw. & Maxon
Polytaenium feei (Schaffn.) Maxon
Pteridium arachnoideum (Kaulf.) Maxon
Pteris hexagona (L.) Proctor
P. longifolia Proctor
P. quadriaurita Retz.
Rhipidopteris peltata (Sw.) Schott.
Tectaria incisa Cav.
Thelypteria asterothrix (Fee) Proctor
T. decussata (L.) Proctor
T. deltoidea (Sw.) Proctor
T. heteroclita (Desv) Proctor
T. oligophylla (Maxon) Proctor
T. patens (Sw.) Small
T. sagittata (Sw.) Proctor
T. serrulata (Sw.) Proctor
T. venusta (Hew) Proctor
Trichomanes crinitum Sw.
T. crispum L.
T. holopterum Kunze
T. hymenophylloides v. d. B.
T. osmundoides DC. ex. Poir
T. rigidum Sw.
T. scandens L.
Trismeria trifoliata (L.) Diels

The Ecological Society of America

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